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Connecting silvan and lacustrine ecosystems: transport of carbon from forests to adjacent water bodies

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Academic dissertation

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ABSTRACT

The carbon cycle and hydrological cycle are closely connected and combine terrestrial and aquatic ecosystems. This study focuses on important processes of the carbon cycle at plant, ecosystem and landscape levels. Carbon allocation was investigated at the seedling scale with microcosm experiments, and carbon fluxes, especially the lateral carbon fluxes from soil to adjacent water bodies, at field sites. The carbon allocation pattern differed between typical boreal tree species, but an increase in temperature did not change the net growth of seedlings, because both photosynthesis and respiration increased similarly and compensated for each other. A higher temperature did not change the species composition of ectomychorrhizal fungi, but some symbiotic fungal species can alter carbon allocation at the plant scale.

This study demonstrates that CO_2 efflux from the soil is largely controlled by biological processes (i.e. the rate of photosynthesis and decomposition), whereas aquatic CO_2 emissions are mostly affected by physical forces (i.e. convection controlling stratification). Lateral carbon flux from soil to the study lake and brook was regulated by hydrology and closely connected to the riparian zone. DOC concentrations in the brook were controlled by precipitation and DOC concentrations in the soil, and rain events increased CO_2 concentrations both in the riparian zone and in the brook. The large water volume of the lake buffered it against changes.

It is of crucial importance to consider terrestrial and aquatic ecosystems together, since lakes and rivers act as significant pathways for terrestrially bound carbon back to the atmosphere. In the natural old-growth forest of this study, lateral carbon transport accounted for 50% and brook discharge for 19% of the terrestrial net ecosystem exchange. Thus, exclusion of the lateral carbon flux would lead to overestimation of the role of the forest as a carbon sink. However, the role of lateral transport can be less important in younger or managed forests, which are faster growing.

Key words (max. 6): catchment, boreal, riparian, carbon balance, lateral carbon flux

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LIST OF ORIGINAL ARTICLES

The thesis is based on the following research articles, which are referred to in the text by their Roman numerals. The articles are reproduced with the kind permission of the publishers. The summary also includes data not published elsewhere.

I Pumpanen, J., Heinonsalo, J., Rasilo, T., Villemot, J. & Ilvesniemi, H. 2012. The effects of soil and air temperature on CO_2 exchange and net biomass accumulation in Norway spruce, Scots pine and silver birch seedlings. Tree Physiology 32: 724–36.
doi:10.1093/treephys/tps007.

II Heinonsalo, J., Pumpanen, J., Rasilo, T., Hurme, K.-R. & Ilvesniemi, H. 2010. Carbon partitioning in ectomycorrhizal Scots pine seedlings. Soil Biology & Biochemistry 42: 1614–1623.
doi: 10.1016/j.soilbio.2010.06.003

III Pumpanen, J., Heinonsalo, J., Rasilo, T., Hurme, K.-R. & Ilvesniemi ,H. 2009. Carbon balance and allocation of assimilated CO_2 in Scots pine, Norway spruce and Silver birch seedlings determined with gas exchange measurements and ^{14}C pulse labelling. Trees-Structure and Function 23:611–621.
doi:10.1007/s00468-008-0306-8

IV Susiluoto, S., Rasilo, T., Pumpanen, J. & Berninger, F. 2008. Effects of grazing on the vegetation structure and carbon dioxide exchange of a Fennoscandian fell ecosystem. Arctic, Antarctic and Alpine Research. 40: 422–431.
doi:10.1657/1523-0430(07-035)[SUSILUOTO]2.0.CO;2

V Rasilo, T., Ojala, A., Huotari, J & Pumpanen, J. 2012. Rain induced changes in CO_2 concentrations in the soil – lake – brook continuum of a boreal forested catchment. Vadoze Zone Journal 11.
doi: 10.2136/vzj2011.0039.

VI Rasilo, T., Ojala, A., Huotari, J., Starr, M. & Pumpanen, J. Concentrations and quality of DOC along a terrestrial-aquatic continuum in a boreal forested catchment (manuscript).

VII Huotari, J., Ojala, A., Peltomaa, E., Nordbo, A. Launiainen, S., Pumpanen, J., Rasilo, T., Hari, P. & Vesala T. 2011. Long-term direct CO_2 flux measurements over a boreal lake: Five years of eddy covariance data. Geophysical Research Letters 38: L18401.
doi:10.1029/2011GL048753.

Authors's contribution:

I–III T. Rasilo participated in the planning of the research and was responsible for the main part of the measurements (except ECM fungal community analysis), and participated in data analysis and the writing process.

IV T. Rasilo participated in the planning of the research, was responsible for the clipping experiment measurements and data analysis and wrote those parts of the article concerning clipping. She also participated in the writing of the rest of the article. The article will also be included in the doctoral thesis of Sanna Susiluoto.

V–VI T. Rasilo was the main author, participated in the planning of the research and was responsible for the measurements and data analysis.

VII T. Rasilo was responsible for the measurements of terrestrial CO_2 and data analysis, and commented on the text. The article was included in the doctoral thesis of Jussi Huotari.

TABLE OF CONTENT

INTRODUCTION

Climate change and its effect on the carbon cycle

The carbon dioxide (CO_2) concentration in the atmosphere has markedly increased during the last century (e.g. Keeling & Whorf 2005, Hoffman et al. 2009). Human influence, including the use of fossil fuels and changes in land use, is behind this increase (IPCC 2007). Short-wave solar radiation penetrates the atmosphere and warms surfaces on the Earth, which then reflects long-wave radiation back to the atmosphere. The greenhouse gas effect refers to the trapping of this radiation by gas molecules. CO_2 and especially methane (CH_4) are effective in trapping long-wave radiation, although the most important greenhouse gas is water vapour. The greenhouse gas effect and the consequent warming are essential for life on Earth in its present form, but human influence has increased the effect and the change is currently rapid. This is nowadays referred to as climate change.

Several climatic scenarios have been prepared, and many of them predict that the temperature increase will be most pronounced at northern latitudes (Christensen et al. 2007). Climate change could drastically affect hydrological conditions and result, for instance, in changes in the amount and timing of precipitation (Trenberth et al. 2003, Trenberth et al. 2007). Some parts of the Earth might suffer from aridity while other parts may become prone to abundant rains with storms and floods. For northern latitudes, the scenarios predict increased winter precipitation and changes in the amount of precipitation falling as snow. The duration of the snow cover might also shorten (IPCC 2007).

Climate change could affect the carbon cycle in numerous ways. The increased concentration of atmospheric CO_2 could enhance photosynthesis, since the uptake of CO_2 will become easier (Tissue et al. 1997, Kirschbaum 2011). This might lead to a reduced need for water. As a result of warmer and longer growing seasons, the amount of assimilated CO_2 could increase. On the other hand, decomposition, which is often controlled by temperature, could also increase as a function of rising temperature (Frierer et al. 2005, Davidson & Janssens 2006). Increases in photosynthesis and decomposition could thus compensate for each other, so that the carbon storage in the soil may not necessarily change. However, even a small change in the equilibrium state could alter the situation, and in the boreal zone, where the carbon storage in the soil is vast, totalling 417 Pg C (Lal 2005), it could have significant effects.

Lateral fluxes connect important components of the carbon cycle and combine different environments. These fluxes are mainly controlled by hydrology, and changes in precipitation are therefore crucial to carbon transport from terrestrial to aquatic ecosystems. For instance, winters are periods of low DOC fluxes, since the soil is frozen and covered with snow, and snowmelt peaks in the spring divide the annual flow regimes in the boreal zone (Ågren et al. 2010). The largest DOC loads are, however, connected with extremely high rain events in the summer (Boyer et al. 1997), when abundant fresh DOC is available. More rapid decomposition due to higher temperatures transforming plant litter to more easily dissolving compounds together with abundant rains can increase DOC transport from soils to adjacent water bodies (Köhler et al. 2009, Sebestyen et al. 2009).

Carbon cycle

In the atmosphere, carbon mainly occurs in the form of CO_2. Currently, the atmospheric CO_2 concentration is 391 ppm (Blasing 2012). There are also other gases that contain carbon, such as CH_4, volatile organic compounds (VOC) and other carbon-containing compounds (e.g. pollen, dust), but in terms of the carbon cycle, CO_2 is the most important component. The concentration of CH_4 is only 1.8 ppm (Blasing 2012) and thus minor compared to CO_2, but CH_4 is a ca. 25 times stronger greenhouse gas (i.e. has higher radiative forcing) than CO_2. Similarly, although the concentration of VOCs in the atmosphere is very low, i.e. in the order of magnitude of ppt (Haapanala et al. 2007), their climatic effects can be considerable through cloud formation processes (Peñuelas & Staudt 2010). As a result of natural and human-induced combustion, black carbon (soot) also exists in the atmosphere. Even though black carbon is biologically inert, it affects the incoming solar irradiation and Earth's albedo and also takes part in aerosol formation (Ramathan & Carmichael 2008). The global annual emissions of black carbon are approximately 8 Tg yr^{-1} and its radiative forcing is more than half of that of CO_2 (Ramathan & Carmichael 2008).

Photosynthetic organisms, mainly plants, contain large amounts of carbon, but the carbon biomass acts differently in terrestrial and aquatic environments. In terrestrial ecosystems, carbon often accumulates in the biomass for decades, and stores in trunks, branches, leaves or needles and roots contain a significant amount of carbon. Conversely, in aquatic ecosystems the turnover of the living biomass is rapid and no carbon accumulation therefore occurs. The main reason for the difference is that in aquatic environments photosynthetic organisms, especially submerged plants and phytoplankton, do not need supporting structures, and there is consequently no accumulation of carbon in lignin or cellulose. Instead, in aquatic ecosystems, carbon accumulates in the sediments. In terrestrial ecosystems, the biomass is divided into above- and belowground components. The division of living biomass into these components depends on the vegetation type, but in boreal forests about 20% of the biomass exists below ground (Helmisaari et al. 2002, Næsset & Gobakken 2008). In forest ecosystems, the carbon stores in the biomass are rather stable and annual variation is limited, whereas in aquatic systems the seasonal succession of phytoplankton is clear and annual variation is thus large (Winder & Cloern 2010). For instance, during the spring diatom bloom there is an abundance of phytoplankton, whereas in winter the amount of photosynthetic plankton is very low.

Soils have the largest carbon reservoirs on Earth. Especially at northern latitudes, with a cool climate and thus low evaporation in comparison to precipitation, the organic humus layer is often thick, and the soil carbon storage can be as much as 85% of the terrestrial carbon stock (Dixon et al. 1994). In boreal forests, vegetation contains 64 Mg C ha^{-1}, whereas soils contain 343 Mg C ha^{-1} (Lal 2005). The accumulation of organic matter in soil is especially great in peatlands, where decomposition is slow due to high humidity and a high water table combined with a low oxygen content and low temperatures. Organic carbon in soils exists in many forms, from simple compounds to complex structures such as humic acids. Inorganic carbon in soils is in a gaseous form (CO_2 and CH_4) in soil air or dissolved in soil water or groundwater. Carbon reservoirs in mineral soils are even greater, but the carbon is mostly in an inorganic, not an organic form. Weathering transforms this carbon to forms that can take part in lateral fluxes, and volcanic eruptions release mineral carbon into the atmosphere. Minerals, together with fossil coal, oil and natural gas, contain 65 000 Gt of carbon (IPCC 2007), but if left untouched, this storage would be permanent.

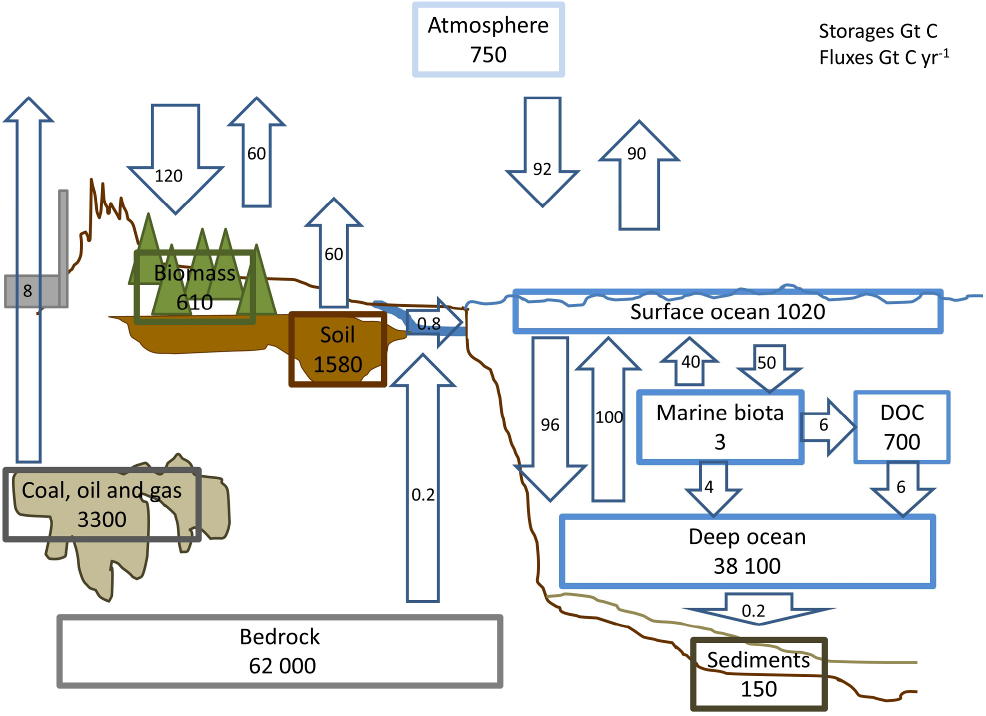

Figure 1. Global carbon storages (boxes, Gt C) and fluxes (arrows, Gt C yr^{-1}) according to IPCC 2001.

Carbon in water, including soil water, can occur in particulate (organic or inorganic POC, PIC), dissolved (DIC, DOC) or gaseous forms (free CO_2, CH_4). Dissolved inorganic carbon is related to gaseous carbon via the carbon equilibrium (Wetzel 2001). The dissolved CO_2 is in the form of free CO_2 or carbonic acid (H_2CO_3), which forms bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) ions. The proportion of HCO_3^- and CO_3^{2-} and free CO_2 depends on pH and to a lesser extent on temperature (Stumm & Morgan 1981). The HCO_3^- ion is the predominant form of DIC in many lakes and rivers, but in Finland, for example, soils and waters are usually acidic and low in alkalinity, and DIC is mainly in the form of CO_2. DOC consists of different organic compounds, which are still nowadays difficult to characterize. Typically, organic molecules that pass through a 0.45-µm filter are considered as DOC, although 0.2-µm filters are sometimes also used (Hautala et al. 2000, St-Jean 2003).

Carbon cycles between the storages (Fig. 1). Globally, the largest flux of carbon is between the atmosphere and vegetation (e.g. IPCC 2007), i.e. atmospheric CO_2 is incorporated into plant biomass through photosynthesis and released back to the atmosphere through respiration. Plants can also emit carbon as VOCs, but their fluxes are minor compared with CO_2 fluxes. However, VOCs are highly reactive and can have strong indirect effects on the photosynthetic capacity of plants (Aaltonen et al. 2011), and through this on carbon cycling. Although plants do not produce CH_4, they can transport it from anaerobic soil layers directly to the atmosphere (Joabsson et al. 1999).

Photosynthesis consists of light and dark reactions. In light reactions, solar energy is used to produce the highly energetic compounds ATP and ADPH. In dark reactions, this energy is used to convert CO_2 into organic compounds, i.e. carbohydrates such as sugars. The utilization of these photosynthetic products for various purposes is referred to as allocation (Litton et al. 2007). Because higher plants need energy and carbon compounds not only in photosynthetic leaves but also in other parts such as the roots, the assimilated carbon must be transported inside plants and the allocation is divided into above- and belowground compartments (e.g. Carbone et al. 2007). The aboveground parts can be further divided, for instance, into leaves, stems and bark, and belowground parts into coarse roots, fine roots and mycorrhizae (e.g. Keel et al. 2012). Furthermore, carbon allocation can be divided on the basis of function. For example, carbon compounds can be used as an energy source to keep cells alive or they can be invested in growth, i.e. for the growth of leaves, stems and roots, as well as reproduction. The amount of carbon allocated to root growth depends on the species (Peng & Dang 2003), but environmental factors such as the availability of nutrients or the light regime determine how much carbon is allocated to shoot growth compared to root growth (Landhäusser & Lieffers 2001). The age and developmental state of the plant as well as the season also affect allocation (e.g. Genet et al. 2010). A substantial amount of carbon allocated below ground is used to sustain mycorrhizal fungal hyphae (Högberg & Read 2006). Most of the boreal tree species live in symbiosis with mycorrhizal fungi, which can form one-third of the soil microbial biomass (Högberg & Högberg 2002).

The carbon from plant biomass eventually ends up in the soil. Through litterfall, dead leaves, branches and other plant parts enter the top of the soil, but root turnover produces decomposing material directly in the soil. Besides coarse litter, roots produce exudates, which are often easily decomposed compounds (Bertin et al. 2003). In addition to litterfall, carbon from the canopy can enter the soil in throughfall. When rainwater passes through the foliage, carbon can dissolve in the water and percolate to the ground. Moreover, the holes and hollows of the bark of trees offer sheltered environments to many organisms, and water flowing down the trunk therefore contains large amounts of DOC (e.g. Moore 2003). Through grazing, a part of the assimilated carbon also ends up in the soil either as faeces or carcasses, or returns to the atmosphere following respiration by animal cells.

Aquatic ecosystems gain carbon from autochthonous production as well as from allochthonous sources (e.g. Jansson et al. 2000). Carbon enters aquatic food webs via the photosynthesis of aquatic higher plants in the littoral zone or unicellular phytoplankton throughout the photic zone of the pelagic ecosystem. Higher plants directly assimilate CO_2 from the atmosphere, similarly to terrestrial plants, but phytoplankton use inorganic carbon dissolved in water. The carbon bound by photosynthesis in aquatic environments is called autochthonous carbon. However, especially in the boreal zone, the load of allochthonous carbon from the surrounding terrestrial ecosystems is of great importance, rendering the systems net heterotrophic (e.g. Jansson et al. 2000). Litterfall and its gradual decomposition in streams is the classical example of the connection between terrestrial and aquatic ecosystems (Vannote et al. 1980).

In addition to coarse litter, carbon can enter aquatic environments in a dissolved form, i.e. as DOC, but also in DIC. DOC has many origins: it can dissolve in water vapour in the atmosphere and reach aquatic systems through precipitation, or originate from living vegetation when rain flushes canopies. It can also originate from litter, soil organic matter, plant roots or fungi when water percolates through soil horizons, or it might be of aquatic origin and thus autochthonously produced by photosynthetic organisms. The DOC concentration is usually lowest in rainwater and increases when the water passes through the canopy (Michalzik & Matzner 1999). The highest DOC concentrations have been found in soil water, although the DOC concentration in soil water decreases with increasing depth (Wu et al. 2010). DOC is removed from the soil solution by decomposition or adsorption. Soil and groundwater entering aquatic ecosystems are often enriched with DIC produced mainly in the mineralization of carbon. A considerable amount (up to 90%) of this terrestrial DIC can be released to the atmosphere through surface waters (e.g. Öquist et al. 2009).

From soils, sediments and surface waters, carbon returns into the atmosphere when the organic compounds are decomposed. In decomposition, the organic material is gradually transformed to compounds with a lower molecular weight, which are finally respired as CO_2 and CH_4. The formed gaseous end products diffuse through the soil and sediment layers and are transported through the water column up to the air. However, organic compounds can also form new even more complex compounds that are highly resistant to decomposition. Such compounds, including humic and fulvic acids, are typical of boreal forest soils.

The production of CO_2 in soil is mainly influenced by root density, microbial community composition, the quality and quantity of soil carbon pools, and photosynthetic activity (Kuzyakov 2006), whereas the transport of CO_2 by diffusion is affected by soil moisture, soil texture and bulk density (Šimůnek & Suarez 1993; Moldrup et al. 1999; Pumpanen et al. 2003). CH_4 is the end product of decomposition in anaerobic conditions such as waterlogged soils or bottom sediments of lakes, where it is produced by methanogenic Archaea (Capone & Kiene 1988, Conrad 2009). However, the rate of CH_4 production is generally much higher than CH_4 emission, because a significant proportion of the produced CH_4 is oxidized to CO_2 by methanotrophic microorganisms before it enters the atmosphere (Reeburgh 2003). Thus, although soils usually act as a sink for atmospheric CH_4 (Conrad 2009), wetlands are important sources of CH_4 (Conrad 2009) and lakes can emit substantial amounts of CH_4 by ebullition.

Hydrology

The carbon cycle and the hydrological cycle are closely linked. Water enters ecosystems in precipitation and infiltrates the soil or flows on the surface to water channels, which finally reach rivers and oceans. Water can return to the atmosphere in any phase of its cycle. There is always evaporation and plants also release water into the atmosphere through transpiration. Water is used in photosynthesis and is reformed in respiration. In addition, water serves as an important transport medium for carbon and many nutrients. The availability of water determines the type of vegetation present, but on the other hand, vegetation also modifies the distribution, circulation and quality of water (e.g. Bosch & Hewlett 1982, Brown et al. 2005).

Surface water moving in brooks, streams, rivers and other water channels originates from one or several of the following sources: precipitation, surface or subsurface runoff from the soil, or groundwater. Besides the climate, runoff from the soil is affected by site topography, soil properties, land cover and vegetation (e.g. Zhang et al. 2001, Costa et al. 2003). The forest canopy intercepts rainfall and thus reduces the amount of water on the forest floor (Carlyle-Moses & Gash 2011). The proportion of intercepted precipitation also changes with the intensity of rain; light rain can be almost entirely intercepted, whereas heavy rain flushes down through the canopy (Carlyle-Moses & Gash 2011). Vegetation also increases evapotranspiration compared with bare ground, which also reduces the water runoff potential (e.g. Zhang et al. 2001). The interception capacity varies greatly depending on the season and type of forest (Carlyle-Moses & Gash 2011).

When water reaches the ground it can either infiltrate and percolate downwards or flow towards water channels as surface runoff. Infiltration is a process combining capillary forces, gravity and pressure due to occasional water ponds at the soil surface. The state of the soil affects the rate of infiltration; the rate declines when soil pores of different sizes become filled with water. Soil texture, structure, organic matter content and compaction affect the infiltration capacity as well as the water holding capacity, and thus the ability of water to move on (Green et al. 2003). The root system influences the soil properties, and for a given soil type the infiltration capacity of a forest is usually clearly greater than that of bare ground (Orwin et al. 2010).

Water moves in the soil by gravity and soil water tension gradients from lower to higher soil water tension. However, the soil is not a homogeneous matrix, but there are hollows and pathways through which the water flows more easily. These can be a result of the burrowing activity of animals or they can consist of the remains of decaying roots. Surface and subsurface flows are difficult to separate because subsurface flow can became surface flow again when it moves towards water bodies. Direct runoff from soil often causes peaks in discharge, i.e. in the amount of water leaving the catchment through an outlet. In forest areas, surface flow is often very small, and changes in discharge are thus mainly caused by subsurface flow processes (Hewlett & Troendle 1975). A rising water level also enhances the connection between soils and water bodies.

The total water flux from soils to water bodies can be calculated on the basis of the water balance, but the exact routes of water in soil are difficult to estimate. Since carbon in soil is not evenly distributed, it is also difficult to know how much carbon is transported with water from soil. The movements of water in soil can be studied, for example, with soil water potentials and stable isotopes (e.g. Song et al. 2009) or modelling (e.g. Russo 1988, Kindler et al. 2011). For example, soil hydraulic conductivity models (e.g. Mecke & Ilvesniemi 1999) have been constructed for podsolic soils and enable calculation of the horizontal and vertical movement of soil water. The porosity and hydraulic conductivity in peat is more complex and different from mineral soil (Letts et al. 2000). The model needs information on the soil water content of different soil layers as well as hydraulic properties (e.g. particle size distribution, soil porosity), which are not easy to collect and were not available at our study site.

Landscape level: terrestrial vs. aquatic ecosystems

When considering ecosystems at the landscape level, we cannot make a strict division between terrestrial and aquatic environments. Instead, different types of ecosystems are usually connected with each other and thus form continua. At the aquatic end of the continuum, lakes and rivers are an important part of the landscape. Globally, surface waters cover 4.6 million km^2 of the Earth's continental 'land' surface (>0.3%) (Downing et al. 2006), but in the boreal zone the coverage is much greater. In Finland, lakes cover on average 10% of the land area, but there are regions where the lake cover can exceed 35% (Raatikainen & Kuusisto 1990). Peatlands are the third main feature of the boreal landscape besides lakes and forests. In total, histosols cover over 3 x 10^6 km^2 (~5%) of the boreal zone (International Union of Soil Scientists, 2006) and the carbon storage of peat is vast, totalling about 270–450 Pg C (Gorham 1991, Turunen et al. 2002). This is the majority of the total carbon stored in boreal soils (Rapalee et al. 1998). Usually, boreal peatlands bind CO_2 and emit CH_4, but the spatial variation is large (Frolking et al. 2006). Carbon sequestration in Finnish peatlands is approximately 40 g C m^{-2} yr^{-1} (Minkkinen et al. 2002).

Even though the significance of terrestrial ecosystems as sites of CO_2 uptake is greater than that of lakes, fresh waters act as flowpaths of terrestrial carbon further down the chain of lakes and rivers to the oceans and finally back to the atmosphere. The capacity of boreal forests to bind CO_2 varies depending on the age of the forest, site fertility and environmental conditions (e.g. Kolari et al. 2004, Hyvönen et al. 2007, Goulden et al. 2011). The net primary production of boreal forests is estimated to vary from 52 to 868 g C m^{-2} yr^{-1} (Gower et al. 2001). In Finland, the annual gross primary production of forests can vary from 323 g C m^{-2} yr^{-1} in clear-cut areas to 1072 g C m^{-2} yr^{-1} in 40-year-old stands (Kolari et al. 2004). On the other hand, the photosynthetic carbon fixation by lakes varies from 24 to 52 g C m^{-2} yr^{-1} (Kelly et al. 2001). In boreal lakes, primary production is much lower and varies from 0.03 to 0.15 g C m^{-2} yr^{-1} (Algesten et al. 2003), but besides autochthonous carbon, lakes process allochthonous carbon of terrestrial origin (e.g. Duearte & Prairie 2005). Thus, when the role of a forest as a sink of carbon is considered, and the lateral flux of carbon to water bodies is ignored, the strength of the carbon sink is easily overestimated. It is therefore of crucial importance to consider areas, not only ecosystems.

Algesten et al. (2003) estimated that 30–80% of the terrestrially fixed carbon entering lakes is emitted back to the atmosphere, whereas Cole et al. (2007) estimated that globally almost 2 Pg of carbon enters lakes every year and approximately 40% of this is released to the atmosphere, 10% is sedimented and 50% is finally transported to oceans. Tranvik et al. (2009) estimated that globally the amount of CO_2 released from lakes into the atmosphere is 0.53 Pg C yr^{-1}. Rantakari (2010) estimated that Finnish lakes annually emit a total of 1400 Gg C as CO_2. Thus, CO_2 emissions from fresh waters are an important part of the carbon cycle, and not only in the boreal zone (Richey et al. 2002, Algensten et al. 2004, Kortelainen et al. 2006) but also at the global scale (Tranvik et al. 2009). Rivers and streams can be even more important pathways of terrestrial carbon, but in comparison to lacustrine ecosystems, little information is available on riverine carbon fluxes (Öquist et al. 2009).

Thus, the distinction between terrestrial and aquatic ecosystems is a man-made classification that can help in considering the similarities and differences between the systems, but may preclude us from understanding the connectivity and borderless nature of reality. The conventional view is that the carbon cycle combines terrestrial and aquatic environments in this order, but carbon can also flow in the opposite direction. For example, rivers and the adjacent riparian zones are closely linked through reciprocal flows of invertebrates (Baxter et al. 2005). Often, the larval forms of insects live in aquatic environments, but as adults they emerge into the terrestrial environment. These emergences can form a substantial part of benthic production and are of importance to riparian consumers such as birds, bats, lizards and spiders, and contribute 25–100% of the energy or carbon to such species (e.g. Fausch et al. 2010).

DOC and DIC fluxes (long-term trends in DOC fluxes)

The role of rivers and streams as carbon transporters has been investigated for decades, but studies have usually focused solely on DOC (e.g. Neff et al. 2006, Ågren et al. 2010). However, CO_2 concentrations in soil are high, and the CO_2 dissolves in water that passes through it. Thus, there is also a potential for the waterborne export of DIC/CO_2 from terrestrial ecosystems (e.g. Öquist et al. 2009). In lakes and rivers, CO_2 can then be released into the atmosphere or it can be assimilated by photosynthetic plankton. In the summer, when boreal dimictic lakes are thermally stratified, CO_2 from decomposition accumulates in the hypolimnion and does not reach the euphotic surface layer where photosynthesis takes place (e.g. Huotari 2011). In productive systems, thermal stratification combined with high photosynthesis and thus CO_2 uptake can lead to CO_2 concentrations below the atmospheric equilibrium. DIC input from soils can thus improve the photosynthetic capacity of lakes.

Long-term changes in DOC concentrations occur in surface waters; for instance, an increasing trend has been observed in Europe (Sarkkola et al. 2009, Chapman et al. 2010, Pärn & Mander 2012) as well as in Eastern North America (Findlay 2005, Couture et al. 2012). There are several possible explanations for this. Organic compounds can act as buffers against acidification, and as sulphuric deposition has decreased, the amount of DOC needed to neutralize acidic compounds has decreased. Consequently, more free DOC is available to be transported (Evans et al. 2006, Monteith et al. 2007, Evans et al. 2012). Another factor behind the ascending trend of DOC is climate change (Freeman et al. 2001, Worral & Burt 2007, Larssen et al. 2011). Warmer winters and increased precipitation can enhance not only the transport of DOC from soils to streams, but also decomposition producing carbon compounds that are easily dissolved. Land use changes such as ditching and afforestation are additional explanations for the increased DOC concentration in surface waters (e.g. Amstrong et al. 2010).

The role of the catchment and its land use types on carbon transport has been vigorously assessed. Many studies have shown that the proportion of peatland in the catchment may determine the amount of DOC exported by rivers (e.g. Arvola et al. 2004, Kortelainen et al. 2006). However, all the water from the catchment passes through the riparian zone before entering a water body, and the zone therefore deserves careful study. The riparian zone is a widely heterogeneous belt around lakes and rivers, a veritable link between aquatic and terrestrial environments. Soils, specially organic soil horizons, are the main source of DOC in headwater catchments (e.g. Evans et al. 2007), and processes in the riparian zone determine the DOC concentrations of surface waters (Löfgren & Zetterberg 2011). Some studies have also demonstrated that most of the carbon entering aquatic ecosystems is actually produced in the riparian zone (e.g. Fiebig et al. 1990, Bishop et al. 1994, Grabs et al. 2012), since the carbon fixed further up in the catchment area is usually decomposed and released into the atmosphere before entering aquatic ecosystems. Thus, riparian zones are hotspots with high biological activity (McClain et al. 2003). They can also act as a filter between terrestrial and aquatic ecosystems and have been successfully exploited in water protection against eutrophication due to cropland fertilization (Vought et al. 1994). The Finnish forestry guidelines also advise the leaving of a 3- to 30-m belt of unmanaged forest around lakes and rivers.

Aims of the study

The overall aim of this study was to determine the most important processes affecting the transport of DIC and DOC from terrestrial to aquatic systems. In addition, I assessed how much of the assimilated carbon is allocated belowground and what are the major processes affecting belowground carbon allocation. This study considered the carbon cycle at both the plant level (I–III) and landscape level (V–VII). The aim was to determine the total carbon budget of seedlings of typical boreal tree species (I, II, III). Besides the allocation of the assimilated carbon in general, I examined the effects of temperature and mycorrhizal fungi (I, II, III). My intention was also to determine the amount of assimilated carbon and its partitioning between the below- and aboveground parts, and to assess the rates of these processes (I, II, III). In addition, the contribution of rhizosphere respiration to total soil CO_2 efflux was estimated in the field and the effect of the ground vegetation on the terrestrial carbon balance was approximated (IV). At catchment scale, I studied how DIC and DOC concentrations in the tree–soil–lake–stream continuum vary, and which factors are behind these variations. I examined the variation both temporally and spatially, at interannual and seasonal scales, and compared the riparian zone with the forest further away from the shoreline of a lake. Particular attention was also paid to the effect of weather events (extreme rains) on lateral carbon transfer (V, VI). Methodologically, my aim was to produce new high-resolution measurement data on CO_2 concentrations in the riparian zone soil, and in lake as well as brook water (V, VI, VII). Finally, I estimated the amount of water entering the study lake from the soil and calculated the transport of DIC and DOC from the soil to both the lake and an outflowing brook, and the export from the catchment through the brook.

MATERIAL AND METHODS

Laboratory measurements

Microcosms

The carbon allocation of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abi*es Karst.) and silver birch (*Betula pendula* Roth.) was studied in tree seedlings grown in microcosms. Seedlings for the experiments were germinated from surface-sterilized seeds. Some of them were colonised with fungal mycelia (*Piloderma croceum* (sequence accession number AM910819), *Cenococcum geophilum* (AM910820) or the dark septate endophyte *Phialocephala fortinii* (AJ630032)) for the ectomycorrhizal fungi (ECM) experiment and planted in the microcosms approximately four weeks after inoculation. The microcosms consisted of separate root (polyethylene back plate and Perspex® cover, root chamber 170 x 280 x 4 mm) and shoot (an aluminium back plate and a transparent Perspex® cover) compartments (details in III) with cooling/warming systems. The humus used as the growth medium was collected from boreal forests located in Southern Finland (61°84’ N, 24°26’ E) near the Hyytiälä Forestry Field Station of the University of Helsinki. For pine seedlings, we used humus from Scots pine-dominated forest (aged 120 years), and for Norway spruce and silver birch the humus was obtained from *Myrtillus*-type forest. The soil at the sites consists of podzolized glaciofluvial sand covered with a humus layer. The collected humus was sieved and homogenized using a 4 mm mesh size. The experiment included controls with only humus and humus with seedlings without inoculation (for details, see Heinonsalo et al. 2001, and II). Seedlings were exposed to a day/night photoperiod of 19/5 h and the photon flux density was 170–300 µmol m^{-2} s^{-1} during the day period for seven months/three months before the CO_2 exchange measurements, $^{14}CO_2$ labelling and harvesting for ECM fungi and biomass.

Soil temperature treatment

To allow equal establishment after transplantation, seedlings were grown for ~2 months at 12–16 °C (day) and 6–7 °C (night) before starting the temperature treatment (I). In the temperature treatment, five microcosms (n = 5 for each temperature and tree species) of each tree species were moved to soil temperatures of 7–12 °C, 12–15 °C and 16–22 °C. The temperatures were chosen to represent the average summer soil temperatures in Lapland, Southern Finland and Central Europe, respectively (Yli-Halla & Mokma 1998). Gas exchange was measured after 6–7 months of growth. Measurements of belowground respiration were carried out at temperatures corresponding to the average treatment temperatures of the growth period (11, 16 and 20 °C, referred to here as cold, medium and warm treatments, respectively). The temperature of the shoot chamber was kept 3–4.5 °C higher than the soil temperature to mimic the natural temperature gradient between the soil and aboveground air (Yli-Halla & Mokma 1998).

Gas exchange measurement system

The microcosms consisted of separate root and shoot compartments, and thus allowed measurements of above- and belowground fluxes (III). The system also included a cooling/warming option separately for the shoot/root compartments. For the gas exchange measurements, one microcosm at a time was connected to a measurement system consisting of CO_2 measuring units (infrared gas analysers Li-Cor LI-7000 for the microcosm air flux and Li-Cor LI-840 (both from Li-Cor Inc., Lincoln, Nebraska) for the reference flux), and a light source. Synthetic air with a CO_2 concentration of 380–390 ppm was introduced into the shoot chambers and root microcosms at a flow rate of 0.5 L min^{-1}. The microcosms and the measuring system are described in detail in Pumpanen et al. (2009) (III).

^{14}C labelling

For ^{14}C labelling, shoots of the seedlings were separately enclosed in airtight Perspex® chambers and the radioactive label was released as gaseous $^{14}CO_2$ (on average 20.7 MBq) from an $NaH^{14}CO_3$ source solution by the addition of 0.2 ml of 1 M HCl. The closed chambers were kept in natural light conditions for 100 min and the amount of the ^{14}C label released and non-assimilated label remaining in the shoot chamber was individually quantified for each seedling. The respired CO_2 was trapped with Carbosorb® solution (Packard, Meriden, Connecticut). The shoot compartment was trapped only for the first 30 minutes, but the root side was trapped for seven days at 12-h intervals. After this growing period, microcosms with seedlings were frozen at -20 °C to stop the enzymatic and transport processes and to slow down decomposition. Thawed seedlings and soils were separated into different fractions (needles, stem, bulk soil, mycelial soil, rhizospheric soil, mycorrhizae and root sample; see details in II), which were analysed separately. After dry mass measurements, the fraction samples were combusted at 900 °C in a sample oxidizer (Junitek Oxidizer, Junitek Oy, Turku, Finland) and the released $^{14}CO_2$ was trapped in 16 ml of a 1:1 (v/v) mixture of Carbosorb® and Permafluor® (Packard, Meriden, Connecticut) (Leake et al. 2001). Growth as well as combustion trappings were measured with a Wallac 1411 liquid scintillation counter (Wallac Oy, Turku, Finland).

Field measurements

Study sites

The DOC and DIC concentration and fluxes and the division of the soil CO_2 flux into heterotrophic and autotrophic components were investigated in natural conditions in the field. One study site was in the Evo Nature Reserve area in southern Finland (Fig. 2). The Valkea-Kotinen catchment (61°14' N, 25°04' E) is situated on the Precambrian shield in the south boreal zone. This headwater catchment has belonged to the International Cooperative Programme on Integrated Monitoring of Air Pollution Effects on Ecosystems (ICP IM) since 1987. It was originally chosen because it represents well the boreal zone, its boundaries were easy to define and had no inlets, the effects on aquatic ecosystems are easier to study than in hydrologically more complex systems. The small size of the catchment (ca. 30 ha) also makes the responses to variations in environmental conditions rapid. The distance to the closest city is 43 km, which also makes it a good reference site for studying the natural properties of a headwater catchment. The catchment was protected in 1955 and thus the forest is old and in as natural a state as possible. The only human influence occurs through atmospheric deposition.

The catchment includes a lake (4.1 ha, mean depth 3 m, 156 m a.s.l.) with a small outflowing brook, coniferous forest (19.6 ha) and peatlands (7.9 ha). The annual mean temperature in the area is 3.1 °C, the growing season ($T > 5$ °C) lasts for 160–170 days and the annual mean precipitation is 618 mm. The old growth forest is dominated by Norway spruce with Scots pine and birch (*Betula* spp.). The measurements were mainly conducted in the riparian zone of the lake, which consists of histosol (peat depth > 60 cm) and is dominated by old Norway spruce (1188 stems per ha), Scots pine (594 stems per ha) and birch (340 stems per ha). Bilberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.), and Labrador tea (*Rododendrum tomentosum* (L.) Harmaja) form the ground vegetation, together with mosses (*Pleurozium schreberi* Mitt., *Hylocomium splendens* Schimp., *Sphagnum* spp.).

The other study site was situated in the Värriö Nature Reserve of Eastern Lapland in Finland (Fig. 2). The area mainly consists of boreal coniferous forest dominated by Scots pine and Norway spruce, but the upper slopes of the hills are covered by mountain birch forest (*Betula pubescens* ssp. *czerepanovii* L.). Scattered Scots pines grow among birches and also form the uppermost tree limit (470 m a.s.l.). Fell tops are treeless and dwarf shrubs together with mosses and lichens cover the ground (the vegetation cover is often less than 100%). There is strong grazing pressure from reindeer, whose population is ca. 2.3 animals km^{-2}. The annual mean precipitation in the area is 592 mm and the average annual mean temperature is only -0.9 °C (1971–2000, recorded at the Värriö Research Station, altitude 390 m a.s.l.). The snow cover melts in late May and the growing season ($T > 5$ °C) lasts for less than 120 days.

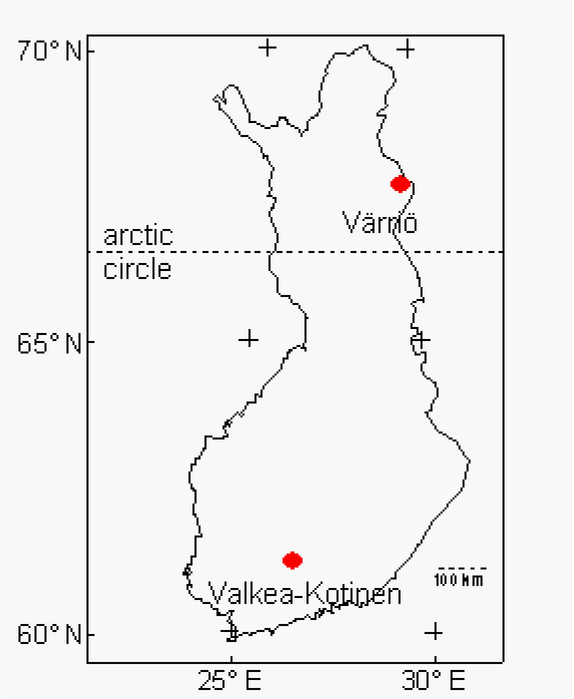

Figure 2. Location of the field study sites in Finland.

The measurements were carried out on Nuortti fell and on Kotovaara hill. Nuortti fell (67°47'N, 29°42'E, 481 m a.s.l.) is treeless and the Finnish-Russian border with a fence preventing reindeer crossing the border passes it. The dominant species in the ground vegetation are lichens (*Cladonia rangiferina* (L.) Nyl., *Cladonia stellaris* (opis) Brodo, *Cladina arbuscula* (Wallr.) Hale&Culb.) together with bog billberry (*Vaccinium uliginosum* L.), lingonberry and dwarf birch (*Betula nana* L.). Bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), black crowberry (*Empetrum nigrum* L.), black bearberry (*Arcostaphylus alpina* (L.) Spreng.), billberry and alpine azalea (*Loiseleuria procumbens* (L.) Desv.) are also present. The lichen cover is <40% on the Finnish side of the reindeer fence and >65% on the Russian side. Kotovaara (67° 45'N', 29° 36'E, 390 m a.s.l.) is covered by pine forest, which was naturally regenerated in the 1950s, and the average tree density and height is 1000 trees ha^{-1} and 8 m, respectively. Dwarf shrubs (*Vaccinium myrtillus* L., *Vaccinium vitis-ideae* L., *Linnea borealis* L., *Empetrum nigrum* L) cover 30% of the forest floor. Mosses (e.g. *Pleurozium schreberi* (Brid.) Mitt.) and lichen (*Cladina stellaris* (Opiz) Brodo) almost completely cover the ground.

Chamber measurements (Värriö, Valkea-Kotinen)

When measuring the rate of CO_2 release, i.e. CO_2 efflux from the soil into the atmosphere, we applied the closed dynamic chamber technique. At Värriö, we used an EGM-4 infrared gas analyser (PP Systems, Hertfordshire, UK) connected to the chamber (diameter 195 mm, height 255 mm) and at Valkea-Kotinen a CARBOCAP® GMP343 infrared diffusion type sensor (Vaisala Oyj, Finland) installed inside the chamber (diameter 190 mm, height 240 mm). Both chambers were covered with aluminium foil and equipped with a fan to ensure air mixing in the chamber. For measurements, plastic collars were installed in the soil at depths of a few centimetres. Chambers were placed on the collars for four minutes and the increase in the CO_2 concentration inside each chamber was recorded. The soil CO_2 flux was calculated from the slope of the linear fit between 60 to 280 seconds starting from the placement of the chamber. The first minute was excluded, since it was assumed that the system had not yet stabilized, and the last minute was omitted to avoid the effect of saturation.

Clipping experiment (Värriö)

The soil CO_2 flux is a result of autotrophic respiration in the rhizosphere and heterotrophic bulk respiration from the decomposition of organic matter. Rhizosphere respiration comprises both the respiration of living roots and the respiration of rhizosphere microorganisms, which directly use photosynthetic products produced by the plant. Bulk respiration is composed of CO_2 released from the decomposition of dead organic matter by soil microorganisms living further away from the roots. We used a trench-plot method to assess the partitioning of soil CO_2 efflux between rhizotrophic and bulk decomposition components. Aboveground vegetation was removed from the collars by clipping, and the roots growing into the collars were cut by digging a 15- to 20-cm-deep trench around the collar. The soil CO_2 flux was measured with the method described above immediately after the trenching, and one and two months later.

Automatic CO_2 measurements (Valkea-Kotinen)

We intended to follow short-term variation in the CO_2 concentration in the stream, lake and the adjacent riparian zone and the effect of extreme weather events on the concentrations in different compartments. Therefore, we opted for automatic continuous measuring systems. Even though the spatial cover is limited with the automatic system, the time resolution is superior in comparison to manual sampling systems. For the automatic CO_2 measurements we installed sensors in the riparian zone soil, the lake and the brook in the Valkea-Kotinen catchment. Two pits (2 m from the shoreline and 150 m apart from each other) were excavated in the soil and Vaisala CARBOCAP® GMM221 diffusion-type CO_2 probes with soil adapters (item number 211921GM, Vaisala Oyj, Finland) were installed at depths of 10 and 30 cm. In addition, a Vaisala CARBOCAP® GMP343 diffusion-type CO_2 probe (Vaisala Oyj, Finland) was installed at 2 cm depth to measure the CO_2 concentration in the soil surface. In the lake, the measurement system consisted of a stainless steel tube going to the target depth (0.1 m, 0.5 m, 1.5 m, 2.0 m and 3.0 m), a silicon tube at the target depth to enable gas transfer between the water and the air inside the tube, and a pump circulating air to the sensors placed in an insulated box on a raft. A similar system was installed in the brook, where there were two measurement points at 10 cm depth and 150 m apart from each other. Temperature was also continuously measured at the same depths as the CO_2 concentration.

Manual gas measurements (CO_2, CH_4) (Valkea-Kotinen)

To study the spatial variation in the soil CO_2 concentration, we installed gas sampling systems in the riparian zone of Lake Valkea-Kotinen. The sampling systems were located 2 m and 12 m from the shore. One system consisted of steel tubes going to the measurement depth (2 cm, 10 cm, 30 cm and 50 cm), a silicon tube enabling gas exchange with the soil air, three-way valves for gas collection and one syringe connected permanently to the tubes to ensure that the volume of the sample was large enough. The sample was taken with a syringe and immediately injected into a vacuumed vial. The vial (volume 11 ml) was overpressurized with approximately 30 ml of sample air. The samples were analysed with a gas chromatograph (Network GC systems 6890N, Agilent Technologies, Santa Clara, CA) for CO_2 and CH_4.

Water sampling and DOC and DIC measurements (Valkea-Kotinen)

To follow the DOC concentration changes in the water as it passes through the canopy–forest floor–soil–lake–brook continuum, we took water samples from precipitation (P), throughfall (TF), soil water at depths of 10 and 30 cm (S10 and S30, respectively), groundwater (GW), lake water (L) and brook water (B). P and TF samples were collected with polyethylene funnels (diameter 197 mm, 130 cm above the forest floor), S10 and S30 with lysimeters (model 653X01-B02M2; Soilmoisture Equipment Corporation, California, USA), GW with a perforated plastic tube (20 mm diameter), L with a tube sampler (volume 2.1 L, length 30 cm) and B directly into a 200-ml plastic bottle. Samples were taken at intervals of one (2007 and 2008) or two (2009) weeks.

To determine the DOC concentrations, the samples were filtered (GF/C, Whatman, Maidstone, UK and Millex-HA 0.45 µm, Merck Millipore, Billerica, Massachusetts) and analysed immediately or frozen (-20 °C). DOC was determined with a total organic carbon analyser (TOC-5000A, Shimadzu Corporation, Kyoto, Japan). Before the analysis, the samples were acidified by adding 30 µl hydrochloric acid (2 mol L^{-1}) to 10 ml of sample to purge inorganic carbon from the water.

DIC was measured from the groundwater and brook water samples using the so-called head space technique. A water sample of 30 ml was taken with a syringe and transported to the laboratory in ice. Syringes were warmed to 20 °C in water bath and 30 ml of N_2 was added. The syringes were shaken for two minutes to ensure the diffusion of CO_2 and CH_4 to the air space. The gas phase was injected into the vacuumed vials (11 ml) to overpressurize them and concentrations were measured with a gas chromatograph, similarly to the manual gas samples. There was expected to be an equilibrium between the liquid and gaseous phase. The calculations of the concentration in the sample were based on Henry's law.

Eddy covariance measurements (Valkea-Kotinen)

Eddy covariance (EC) measurements were used to estimate evaporation from the water surface of the lake. EC measurements were also used for the CO_2 flux, which was compared with the fluxes calculated from the concentrations in the water (VII). The EC apparatus was placed on a raft with three floats approximately 280 m away from the northwest end of the lake and 35 m from the eastern shore. The surface of the raft was 0.35 m above the lake surface and the EC measurement tower pointed to the longest fetch. The EC measurement system consisted of a Metek ultrasonic anemometer (USA-1, Metek

GmbH, Germany) to measure the three wind speed components, and a closed-path infrared gas analyser (LI-7000, Li-Cor, Inc., Lincoln, Nebraska, USA) that measures CO_2 and H_2O concentrations. The measurement height was 1.5 m and sampling frequency was 20 Hz (Vesala et al. 2006). The micrometeorological fluxes of heat, CO_2, H_2O and momentum were calculated as covariances between the scalars (temperature or mixing ratio) or horizontal wind speed and vertical wind speed according to commonly accepted procedures (Aubinet et al. 2000).

Calculations and analysis

Calculation of carbon fluxes

We used modelling to estimate the photosynthesis and respiration of the forest in the catchment. The forest in the riparian zone was measured in three study plots of 78.5 m^2 placed on the study transects. We calculated photosynthesis and foliage respiration using stand gas exchange model SPP (Mäkelä et al. 2006) with measured (tree density, average height) and calculated (foliage biomass) (Repola 2008, 2009) tree data. Air temperature and precipitation data from the Finnish Meteorological Institute (Lammi Biological Station) and PAR data from SMEARII (Hyytiälä Forestry Field Station) were used to run the model. Soil humidity measurements (VI) showed that soil was never dry and thus the effect of soil moisture was not taken into account. The model calculates the amount of incoming irradiance and its attenuation in the canopy, and based on this the amount of photosynthesis was estimated. The SPP model also gives values for respiration and transpiration. The model consists of an irradiance model and a shoot photosynthesis model. In the irradiance model, the canopy consists of randomly distributed identical trees, and tree crowns are described as ellipsoids or cones filled with randomly distributed shoots. Shoot photosynthesis is calculated with the optimal stomatal control model (Hari et al. 1986, Hari & Mäkelä 2003) using the irradiance, ambient temperature and air humidity. The model of temperature-driven annual cycle (Mäkelä et al. 2004) was used to calculate the seasonal course of photosynthetic capacity.

The soil CO_2 flux was studied with chamber measurements. To calculate the annual soil CO_2 flux, an exponential curve was fitted to the temperature and chamber measurement data and the obtained formula was used to calculate daily values from the continuous temperature measurements. These were then summed to obtain the annual CO_2 flux.

The proportion of root and rhizosphere respiration in relation to the total soil CO_2 flux was estimated in the Värriö experiment from the relative change in the respiration rate after trenching and the removal of vegetation. The ratio of respiration from the control and treatment collar at a given moment was compared with their ratio before trenching and the removal of vegetation.

We used the water balance approach to calculate water fluxes. Daily discharge (R) and precipitation (P) values were obtained from the Finnish Environment Institute and the Finnish Meteorological Institute, respectively. The difference between R and P was considered to represent the evapotranspiration (ET) of the total catchment (c) by assuming that there were no changes in the water storage (ΔS) or leakage of water from the catchment through another pathway besides the brook ($P_c = R + ET_c + \Delta S_c$). The water fluxes of the terrestrial part of the catchment (t) can be described as $P_t = ET_t + IF + \Delta S_t$ and the aquatic part (a) as $P_a + IF = ET_a + R + \Delta S_a$, where IF is the lateral water flow from the soil into the lake. The evapotranspiration from the lake (ET_a) was calculated from the energy flux measurements with EC (Nordbo et al. 2011). Thus, the evapotranspiration of the forest (ET_t) was determined by subtracting ET_a from ET_c. ($ET_t = ET_c - ET_a$). By assuming that there were no changes in either soil or lake water storages, IF could be calculated. The terrestrial transpiration by vegetation and ground without vegetation was obtained with the SPP model described above. The amount of terrestrial transpiration was subtracted from the total terrestrial evapotranspiration to obtain the terrestrial evaporation.

The export of DOC from the catchment was calculated by multiplying the daily discharge by the interpolated daily DOC concentrations in the brook water. The transfer of DOC from the soil to the brook was estimated as the difference in the DOC fluxes at two measurement points 150 m apart. The flux of DOC from the soil to the lake was estimated from the SW DOC concentrations and the water balance calculations. However, the pathways in the soil through which the water passes before entering the lake remain unknown, and the exact DOC concentrations could not therefore be determined. Consequently, we used the highest and the lowest concentrations in the soil water and groundwater to estimate the possible range of DOC inflow. Similar calculations were also performed for DIC transport based on CO_2 concentrations in the soil at different depths. We assumed that the CO_2 concentration in the soil air was in equilibrium with the CO_2 concentration in the soil water and used Henry's law to convert ppm to g of carbon.

Statistical tests

A general linear model (GLM–UNIANOVA) was used to test the effects of temperature treatment (cold, medium and warm), tree species and their combined effect on carbon allocation, the above- and belowground CO_2 exchange and the species composition of ECM fungi (I). One-way analysis of variance (ANOVA) was used to assess the effect of temperature on all measured parameters within each tree species.

The effects of ECM species on carbon balance were analysed by using stepwise linear regression analysis (II). In the analysis, the presence or absence of different ECM species was used as 'independent' and studied variables (e.g. biomass or label distribution) as 'dependent'.

To identify the possible diurnal pattern in CO_2 concentrations in the studied soil, brook and lake, we applied the Spectral Plot procedure in SPSS 15.0 (IBM Corporation, Somers, NY) (V), which is generally used to identify periodicities in time series (Trimbee & Harris 1983). We removed the seasonal trend by using residuals of linear fitting in the Spectral Plot analysis.

The changes in CO_2 concentrations due to rain events were studied by comparing event periods with reference periods (V). Hourly averages of CO_2 concentrations on seven rainless days preceding the rain event on 8 August 2008 were considered as the reference period. The time delay between the start of the rain and its influence on CO_2 concentrations was determined by comparing the four-hour slopes of the linear regression lines fitted to CO_2 concentrations at one-hour intervals. The time lag was taken as the moment when the slopes for the average 'reference period' and 'event period' first differed from each other ($P < 0.05$). The difference was tested with the Student's *t*-test.

To examine which factors affected DOC concentrations in the brook, we used non-parametric Kendall rank correlations and partial Kendall correlation to determine whether the factors were independent of each other (VI).

RESULTS

Carbon cycle at the plant scale - Microcosm measurements (I, II, III)

Carbon fluxes and allocation in tree seedlings

The maximum photosynthetic capacity (P_{max}) values of silver birch were twice as high as those of Scots pine, and three times higher than Norway spruce when measured under the same temperature and light conditions. P_{max} was 0.60 µg C s^{-1} g^{-1} for Scots pine, 0.33 µg C s^{-1} g^{-1} for Norway spruce and 0.82 µg C s^{-1} g^{-1} for silver birch seedlings (III). According to the pulse labelling experiments, 43–75% of the assimilated carbon remained in the aboveground parts of the seedlings (Fig. 3). The amount of carbon allocated to root and rhizosphere respiration was about 9–26%, and the amount of carbon allocated to root and ectomycorrhizal biomass about 13–21% of the total assimilated CO_2.

The presence of certain mycorrhizal species affected the allocation. When indigenous *Suillus variegatus* was present, significantly more needle and aboveground biomass (cumulative allocation) was measured compared to seedlings without *S. variegatus*. In addition, the root-to-shoot ratio was lower in seedlings containing *S. variegatus* (II). The presence of *C. geophilum*, on the other hand, increased the amount of labelled carbon in bulk soil and decreased its amount in root biomass.

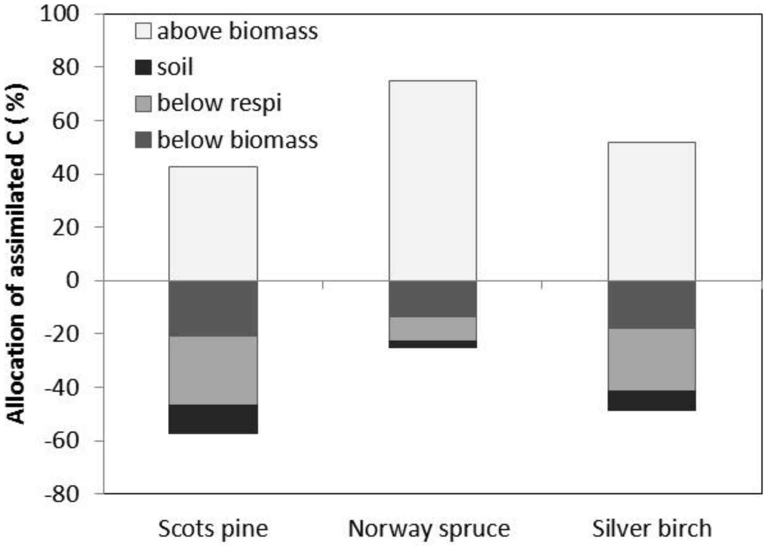

Figure 3. Allocation of assimilated carbon (%) in Scots pine, Norway spruce and silver birch seedlings.

Rate of allocation

In Scots pine and silver birch, the amount of assimilated radioactive carbon started to increase in root and rhizosphere respiration 12 h after labelling, whereas in Norway spruce the increase was visible 24 h after labelling. For silver birch, the respiration clearly peaked within a few days of labelling, while for Norway spruce and Scots pine the rate of respiration of labelled carbon remained at elevated levels for almost a week. In Scots pine as well as in silver birch, most of the labelled carbon passed through the seedlings within the first 3.5 days. Moreover, the larger the mychorrhizal biomass, the faster was the rate of release of the respired carbon. A higher soil temperature increased the rate of respiration of both below and aboveground parts and the rate of photosynthesis. The increases compensated for each other, and the net CO_2 change was not consequently altered at higher temperatures.

Temperature treatment (I)

A higher temperature increased the root biomass and accelerated photosynthesis as well as the respiration of shoots, roots and the rhizosphere. The simultaneous increases compensated for each other, and CO_2 exchange and seedling biomass did not therefore change. A higher temperature did not affect the species composition of ECM fungi, even though the number of ECM per seedling increased. The photosynthesis and both shoot and root respiration at higher temperatures increased most in Norway spruce and silver birch. The total seedling biomass increased as a function of temperature in all three tree species, but the highest values were already observed at 12–15 °C in Norway spruce and silver birch. The shoot-to-root ratio only increased with increasing temperature in silver birch. ECM fungi parameters only showed differences between temperatures in Scots pine, in which the ECM number in relation to the root length decreased with increasing temperature.

Carbon balance at the seedling scale

The tree species behaved differently in terms of carbon exchange in the tree seedlings (III). Silver birch had the highest photosynthetic rate (0.33 and 0.23 $\mu g\ C\ s^{-1}$ at 3 months and 7 months of age, respectively) and Scots pine the lowest (0.04 and 0.08 $\mu g\ C\ s^{-1}$, respectively). The photosynthetic rate of Norway spruce (0.09 and 0.17 $\mu g\ CO_2\ s^{-1}$) was between these values. In the coniferous species the photosynthetic rate increased during the study period, but that of the deciduous silver birch decreased due to the senescence of leaves. The normal growing period in southern Finland is approximately four months and the study period thus exceeded the normal life span of deciduous leaves. A similar phenomenon was also observed for shoot respiration in the dark, which increased in coniferous species but decreased in silver birch. On the other hand, the root and rhizosphere respiration of all the studied species increased during the study period.

The mycorrhizae had a significant effect on both photosynthesis and respiration. When *S. variegatus* was present, there was an increasing trend ($p = 0.264$) in net photosynthesis (II). In addition, the respiration of shoots, roots and the rhizosphere (including mycorrhizae) and total belowground respiration were all higher when *S. variegatus* was present than in microcosms without it. In the presence of indigenous *Laccaria* sp., the photosynthetic efficiency was lower than without it. *P. croceum* did not cause any changes to the studied carbon budget parameters.

Carbon cycle at the catchment scale: Field measurements (IV, V, VI, VII)

Soil CO_2 effluxes in Valkea-Kotinen and Värriö (IV, unpublished data)

Seasonal patterns in soil CO_2 efflux were investigated in the Valkea-Kotinen catchment with old-growth Norway spruce and in the Värriö nature reserve in a Scots pine stand and in open fell vegetation. In Valkea-Kotinen, the soil CO_2 flux varied from 0.01 to 0.82 g C m^{-2} h^{-1} (Fig. 4). The flux was highest in the summer. In Valkea-Kotinen, there was no difference in the soil CO_2 flux in the riparian zone or in the forest, either for the whole year or in specific seasons. In Valkea-Kotinen, the exponential fitting between the measured soil CO_2 flux and temperature (T) resulted in the following equations for the shore (s) and forest (f), respectively: $flux_S = 0.0456*e^{0.1121Ts}$, $R^2 = 0.68$; $flux_F = 0.0466*e^{0.1219Tf}$, $R^2 = 0.69$. Using these equations and daily temperatures, the annual soil CO_2 flux was estimated as 0.87 and 0.95 kg C m^{-2} yr^{-1} in the shore and forest, respectively.

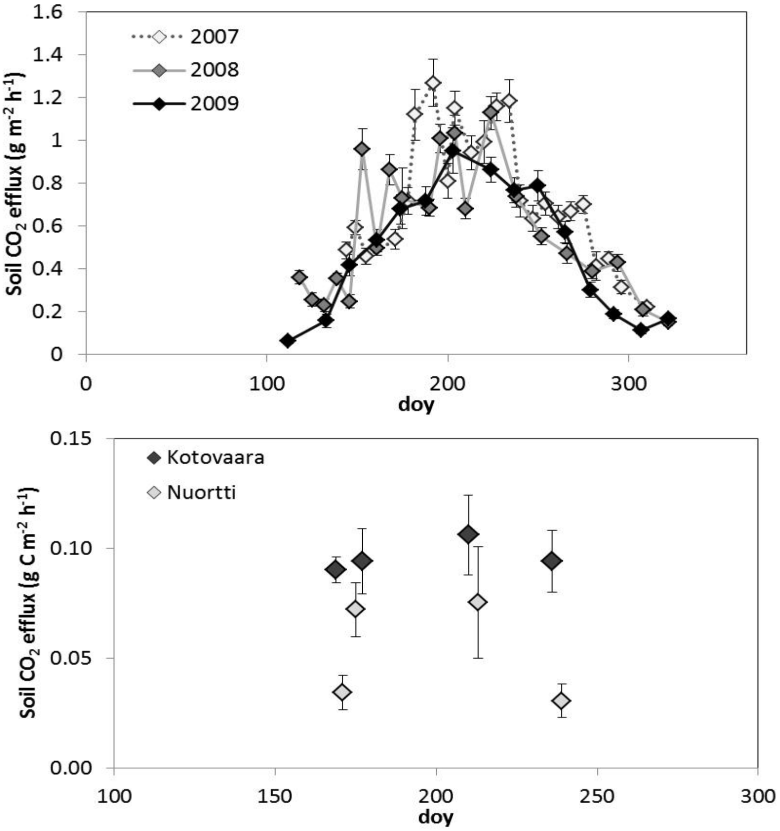

Figure 4. Soil CO_2 flux (g C $m^{-2}h^{-1}$) in the Valkea-Kotinen catchment in 2007–2009 (upper panel) and in Värriö on Kotovaara hill and Nuortti fell 2004 (lower panel). Error bars indicate standard errors (n = 18 in Valkea-Kotinen and n = 8 for both sites in Värriö). Note the different scales.

In Värriö, soil CO_2 fluxes were lower than in Valkea-Kotinen and varied from 0.01 to 0.38 g C m^{-2} h^{-1} (Fig. 4). Fluxes were lower on Nuortti fell (0.05 and 0.03 g C m^{-2} h^{-1}) than on Kotovaara hill (0.09 and 0.09 g C m^{-2} h^{-1}) in June and August, but there was no significant difference in July (0.08 and 0.11 g C m^{-2} h^{-1} for Nuortti and Kotovaara, respectively). In general, the flux was highest in July–August. During the time when the soil temperature was above 5 °C, the CO_2 flux from soil was 0.10 kg C m^{-2} on Nuortti, 0.37 kg C m^{-2} on Kotovaara, and 0.65 kg C m^{-2} on the shore and 0.71 kg C m^{-2} in the forest at Valkea-Kotinen.

Clipping experiment (V, unpublished data)

On Nuortti, the relative respiration rate declined by about 50% during the first week after clipping the vegetation. One month after the clipping, soil respiration started to increase on Nuortti, even though there was variation in respiration between the measurement dates. A similar decline was not observed on Kotovaara, but the respiration in the clipped collars remained higher than in the control collars throughout the study period.

Automatic CO_2 concentration measurements (V)

There was diurnal variation in the surface layer CO_2 concentration in the soil as well in the brook, but the variation disappeared with depth. In the soil, the CO_2 concentration peaked at night and was lowest in the afternoon. The opposite situation was recorded in the lake, where the concentration was highest during the day and lowest after midnight. The variation in the CO_2 concentration of brook water followed that in the lake and peaked in the afternoon.

The rain event changed the normal diurnal pattern in the soil, the lake and the outflowing stream (Fig. 5). In the soil, the CO_2 concentrations increased some hours after the rain event, when water filled the soil pores and slowed down the diffusion of CO_2. A similar phenomenon was observed in the stream, but in the lake the large water volume buffered the changes. Even though the water with a lower CO_2 concentration from the lake diluted the CO_2 concentration in the brook, the input from the soil dominated the flow after the rain event and the CO_2 concentrations increased.

In the soil, the CO_2 concentration was highest in late summer and remained low in winter from November to May. The lake was stratified in the summer, and the CO_2 concentration increased in deeper water layers below the thermocline during the whole summer until the stratification was broken in August-September. Thus, the highest concentrations in the bottom layers occurred in late summer before autumn stratification, but in the surface layer the concentrations were highest after the mixing when CO_2-rich hypolimnetic water was mixed throughout the water column.

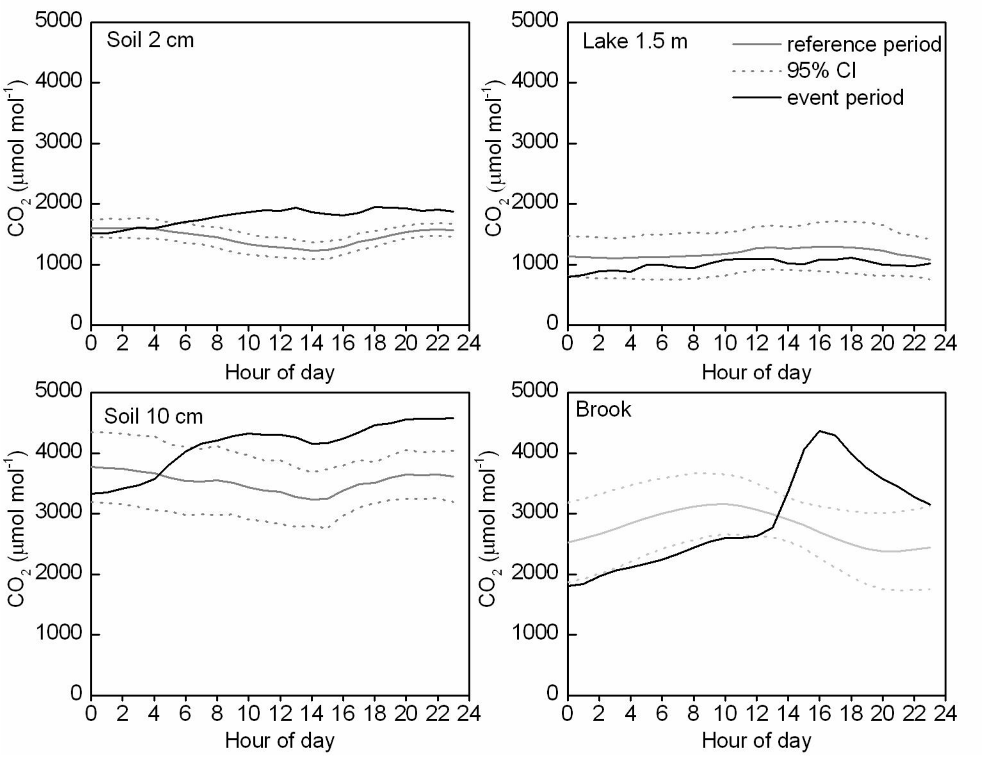

Figure 5. Event-driven changes in CO_2 concentration (µmol mol^{-1}) in the riparian zone of the soil, the adjacent lake and the brook in the Valkea-Kotinen catchment. The reference period is the 7 days preceding the rain event on 8 August 2008.

Manual gas measurements (unpublished data)

CO_2 and CH_4 concentrations varied with depth in both the riparian zone and further up in the forest (Fig. 6). The difference was significant between all the depths, except for CH_4, which differed significantly only between the depths of 30 and 50 cm. Seasonal differences, on the other hand, were mainly significant only for the CO_2 concentrations of the surface layers (2 cm and 10 cm). For CH_4, the difference was only significant at 2 cm between summer and autumn. In contrast to the effect of season, spatial variation was more evident at deeper horizons. Inter-annual variation was most pronounced in the CO_2 concentrations from 10 cm to 50 cm.

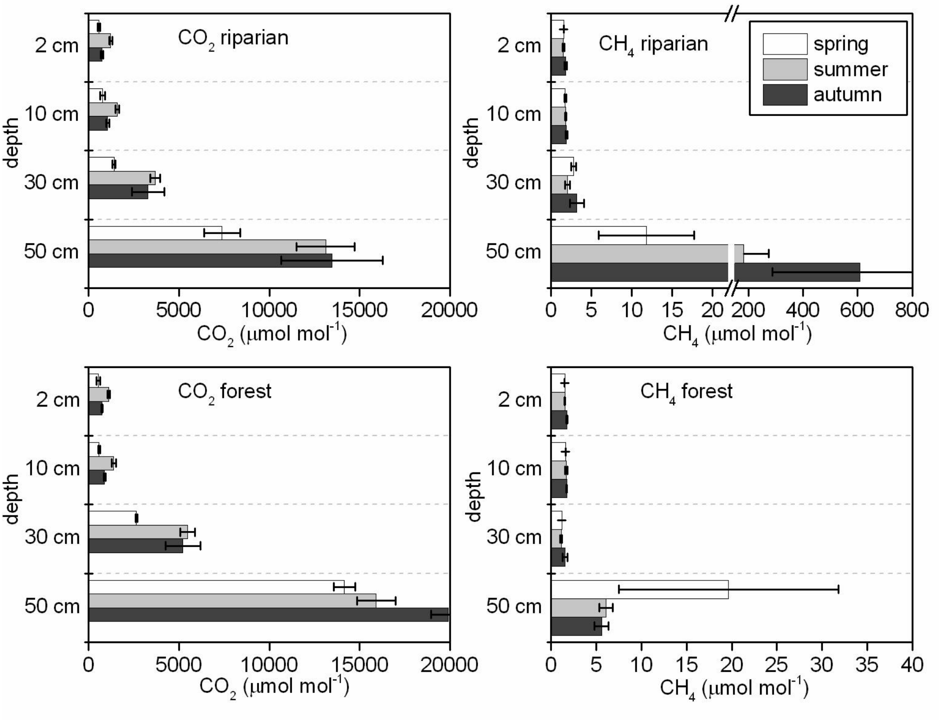

Figure 6. CO$_2$ and CH$_4$ concentrations (ppm) at different depths in the riparian zone soil matrix (2 m from the shore) and in forest soil (12 m from the shore) in the Valkea-Kotinen catchment. Error bars represent standard errors of the mean.

In the groundwater, CO$_2$ concentrations were many times higher than CH$_4$ concentrations. The CH$_4$ concentration was higher in the riparian zone than in the forest, but there was no such spatial difference in the CO$_2$ concentration. On the contrary, the increase in CO$_2$ from the spring towards the autumn was clear, but no significant seasonal variation was observed for CH$_4$.

DOC concentrations (VI)

The mean concentration of DOC varied from 2.4 mg L^{-1} in rainwater to 132.3 mg L^{-1} in riparian soil water (Fig. 7). Soil (132 and 79 mg L^{-1}) and groundwater (53 and 42 mg L^{-1}) concentrations were higher in the riparian zone than in the forest. In the brook, DOC concentrations increased as a function of distance from the lake (mean concentrations 12.5, 14.5, 17.3, 23.6 mg L^{-1} in the lake and at the three brook sites downstream, respectively). The amount of weekly rainfall was positively correlated with the brook water DOC concentration, but negatively correlated with the lake water DOC concentration, indicating that the terrestrial DOC input has an important impact on the brook DOC concentration.

The DOC concentration in the soil water increased during the growing season, but in the surface layers of the lake it was generally stable. In the brook, the concentration varied with the amount of rainfall, which regulated the DOC input from the soil.

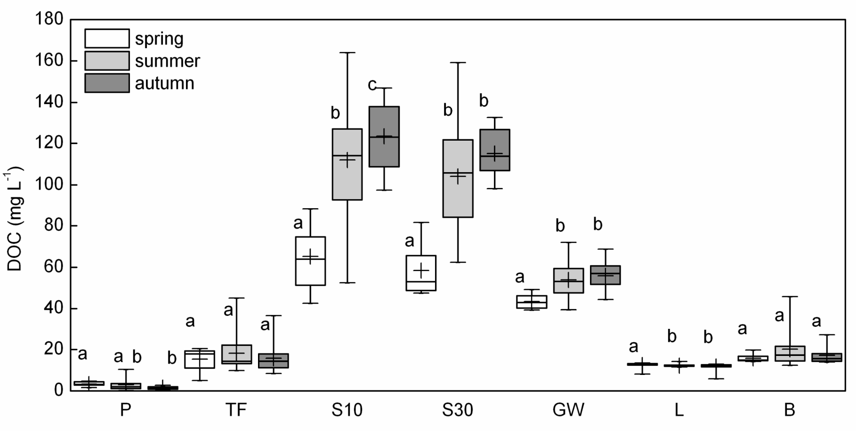

Figure 7. DOC concentrations (mg L^{-1}) in Valkea-Kotinen in 2007–2009. P = precipitation, TF = throughfall, S10 = soil water at 10 cm depth, S30 = soil water at 30 cm depth, GW = ground water, L = lake water, B = brook water. Spring = April–May, summer = June–August, autumn = September–November. Boxes extend from the 25th percentile to the 75th percentile, with the horizontal line at the median (50th percentile) and plus symbols indicate the mean. Whiskers extend down to the lowest value and up to the highest 13 value. Letters indicate the significant difference between seasons.

Eddy covariance measurements (VII)

Seasonal variation was also observed in the role of the lake as a CO_2 source. CO_2 efflux to the atmosphere was highest in late summer during the deepening of the thermocline and during the autumn turnover (0.52–0.56 g C m^{-2} d^{-1}) (VII). The ice melt period and the following often incomplete spring turnover were the other pronounced periods of CO_2 efflux, although their contribution to the annual CO_2 flux was small. In the summer, efflux was usually very low and there were moments when the lake acted as a carbon sink due to active photosynthesis by plankton, which decreased the surface water CO_2 concentration below the atmospheric equilibrium. On the other hand, CO_2 bursts also occurred in the summer due to sudden deepening of the thermocline and CO_2 export from the soil after heavy rains. In the spring the emission rate was 0.31 g C m^{-2} d^{-1} and during summer only 0.14 g C m^{-2} d^{-1}. Thus, spring (ice melt–May) contributed 13%, midsummer (June–July) 10% and late summer and autumn (August–freezing) 77% to the annual CO_2 emission (77 g C m^{-2} yr^{-1}). The CO_2 flux was best explained by the partial pressure of CO_2 in the surface water, which clearly depended on the strength of stratification of the water column. Under stable stratification conditions, the surface partial pressures of CO_2 and consequently CO_2 emissions were low.

Carbon fluxes and total carbon budget at the catchment scale

The lake was a source of carbon every year and the annual CO_2 emissions to the atmosphere were 97, 74, 74, 74 and 68 g C m^{-2} yr^{-1} in 2003, 2004, 2005, 2006 and 2007, respectively (VII). On average, the lake emitted 77 g C m^{-2} yr^{-1}. The CO_2 flux from the forest soil was 963, 913 and 932 g C m^{-2} yr^{-1} for 2007, 2008 and 2009, respectively. Trees photosynthesised 1676, 1674 and 1711 g C m^{-2} yr^{-1} and respired 800, 735 and 695 during the same years. The DOC export through the brook was 3.2, 3.8, 1.3 g C m^{-2} yr^{-1} for 2007, 2008 and 2009, respectively.

The terrestrial area of the catchment gained 410 kg of carbon as DOC in precipitation. Trees and underground vegetation bound a total of 448 400 kg C yr^{-1} and the total ecosystem respiration released 439 800 kg C yr^{-1} (Fig. 8). CH_4 emissions from the soil were probably negligible, because even though CH_4 concentrations were high in the deep soil layers they were close to the atmospheric concentration near the soil surface. Thus, the produced CH_4 was oxidised during diffusion through soil layers or it was laterally transported to the lake; neither of these processes were measured or taken into account in the above calculations. Kindler et al. (2011) also stated that leaching of CH_4 is insignificant compared with other fluxes of carbon. When ignoring lateral carbon transport, these fluxes result in an NEE of 8600 kg C yr^{-1} (33 g C m^{-2} yr^{-1}).

The CO_2 exchange between lake and atmosphere resulted in a flux of 3200 kg C yr^{-1} to the atmosphere. In addition, the CH_4 flux of 54 kg C yr^{-1} (Kankaala et al. 2006) contributed to the export to the atmosphere. The other outputs from the lake were sedimentation (115 kg C yr^{-1}, Pajunen 2004) and transport by the brook (950 kg C yr^{-1} as DOC and 95 kg C yr^{-1} as DIC) (Fig. 8). In addition to autochthonous photosynthesis, the lake gained carbon through DOC in precipitation (65 kg C yr^{-1}) and laterally from soils as DOC and DIC. Other possible carbon input fluxes included DIC in precipitation and in dry deposition, and some carbon could also leave the lake as POC in the outflowing water, but these fluxes were negligible. To close the carbon balance of the lake, the terrestrial input must have been 4400 kg C yr^{-1}. At maximum, 375 kg of this was DIC (V), and thus the terrestrial DOC input was 4025 kg C yr^{-1}. This halves the role of the forest as a carbon sink, as 50% of the terrestrial NEE was lost to the lake and brook.

At the catchment scale, the net CO_2 flux from the atmosphere to the catchment was 5400 kg C yr^{-1}. In addition, 470 kg C yr^{-1} entered the catchment in precipitation. Output through the brook (1050 kg C yr^{-1}), sedimentation (115 kg C yr^{-1}) and the lacustrine CH_4 flux (54 kg C yr^{-1}) were the same as at the lake scale. Thus, the catchment acted as a carbon sink of 4700 kg C yr^{-1} (16 g C m^{-2} yr^{-1}).

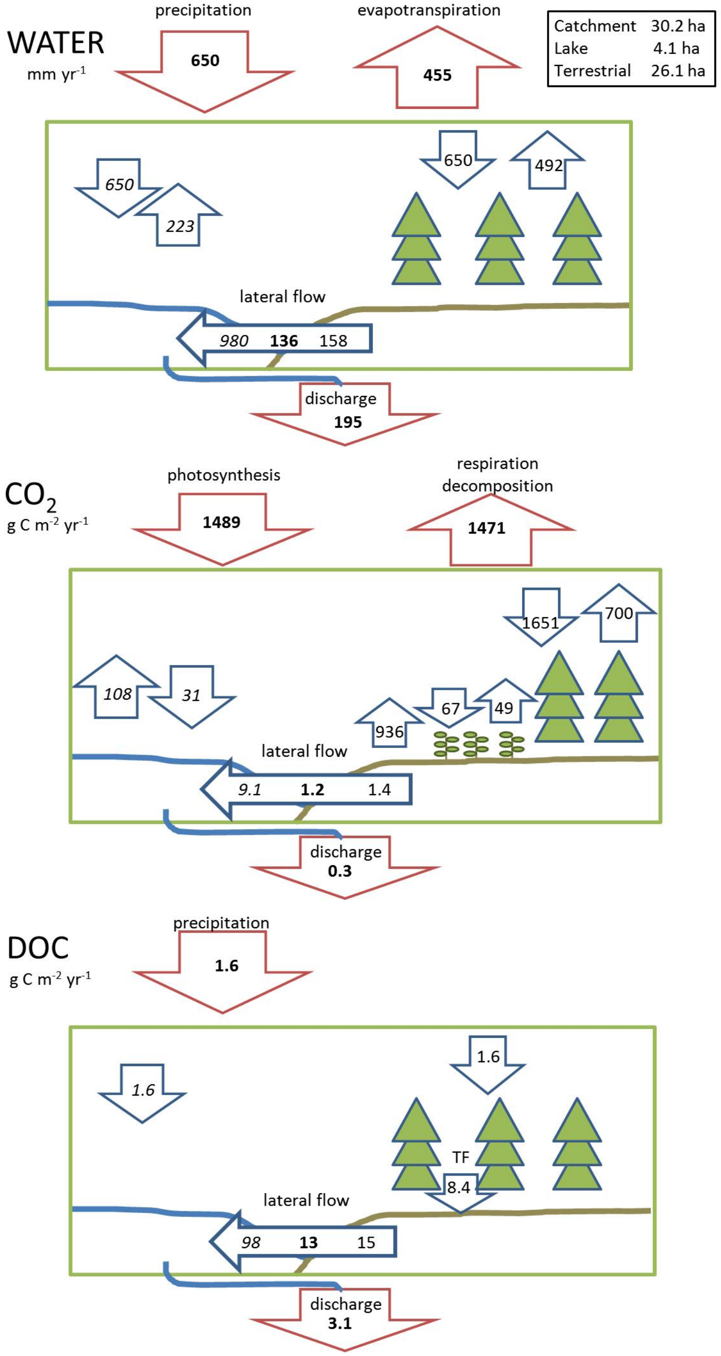

Figure 8. Annual fluxes of water (mm), CO$_2$ and DOC (g C m^{-2}) in the Valkea-Kotinen catchment. Fluxes are calculated separately over the lake area (*italics*), over the terrestrial area (normal) and over the total catchment area (**bolded**).

DISCUSSION

Trees are the main photosynthesizers in boreal ecosystems. The photosynthetic rate and carbon allocation vary between species (I–III). Among the studied tree species, silver birch assimilated carbon most efficiently, and despite high respiration its net CO_2 exchange was also higher than that of Norway spruce and Scots pine (III). The differences in growth patterns reflect the ecology of the species. Pioneer species such as birch and pine grow rapidly after germination, while spruce, as a shade-tolerant species, starts to grow more slowly. Variation in the maximum photosynthetic capacity is also evidence of adaptation to different conditions (III). Even though trees are the main defining feature of forests, the role of ground vegetation cannot be ignored (Kulmala 2011). Although the photosynthetic production of ground vegetation decreases as a function of the age of a forest (Kulmala 2011), it contributes 3–50% to the annual gross primary production of coniferous forests (Goulden & Crill 1997, Subke & Tenhunen 2004, Ilvesniemi et al. 2009). In Valkea-Kotinen, ground vegetation accounted for approximately 4% of the total photosynthesis, but in the fell ecosystems without trees, dwarf shrubs were responsible for most of the photosynthesis and respiration (IV).

In Scots pine seedlings, over 60% of the biomass was allocated belowground (II). The belowground biomass was divided equally between roots and mycorrhizae, indicating that seedlings clearly invest in symbiosis with mycorrhizal fungi (II). In shorter-scale ^{14}C labelling, 48% of the biomass was allocated belowground. The difference between the short-term and long-term allocations suggests that some of the recently bound carbon could be stored in the shoots. Allocation may also vary depending on the growth phase. ^{14}C labelling was carried out at the end of the growing period, and shoot storages could be important in seasonal carbon allocation (Horwarth et al. 1994). In larger trees, the allocation pattern may be different due to increasing storage pools and reproductive functions, which reduces the allocation to growth functions (Genet et al. 2010). For example, carbon demands were proportionately greater and foliar carbon reserves smaller in mature trees than in seedlings of the northern red oak (Samuelson & Kelly 1996).

In Valkea-Kotinen, 56% of the total terrestrial respiration came from the soil. In fell ecosystems, the proportions of root and rhizosphere respiration and heterotrophic respiration were the same (IV). In the microcosms, root and rhizosphere respiration also formed on average approximately half of the total belowground respiration (II, III). The symbiotic mycorrhizae accelerate the turnover rate of carbon and thus have a significant effect on carbon cycling in forest soils (Högberg & Reed 2006). The larger the ECM biomass, the faster was the respiration rate, and carbon escaped from the system to the atmosphere.

At northern latitudes, seasonality is determined by the light and temperature regimes, which control biological processes. Biological processes control carbon cycling and largely affect carbon fluxes. The responses to light as well as the allocation patterns of different tree species were clearly different (III). The allocation pattern also changed when seedlings became older and their phenological stage changed. The seasonality of the soil CO_2 flux is additionally influenced by photosynthesis, as a significant part of the produced CO_2 originates from recently assimilated photosynthesised compounds (Högberg & Reed 2006). The rapid release of labelled carbon from the belowground component shows how tightly photosynthesis controls soil respiration and indicates that recent photosynthates play a significant role in soil CO_2 efflux (II). Microbial activity increases with increasing temperature, and decomposition is thus also correlated with seasonal temperature changes (Robinson 2002, Baldrian et al. 2012). As the soil CO_2 flux reflects not only biological processes but also physical processes controlling the diffusion rate, it is additionally affected by soil humidity and its seasonal changes.

In terrestrial ecosystems, the rate of CO_2 production is usually higher than in aquatic ecosystems due to the production of large amounts of fresh organic matter by vegetation. In Valkea-Kotinen, soil CO_2 efflux was approximately ten times greater than the atmospheric CO_2 flux from the lake. Soil CO_2 efflux is often explained by temperature, which affects the rate of CO_2 production. Precipitation can alter soil CO_2 efflux by slowing down diffusion or by flushing CO_2 towards water bodies. However, soil in which water movement is restricted by small pores is a more stable system than a lake, and thus the changes are slower. Soil CO_2 efflux depends more on biological processes such as photosynthesis, decomposition and the presence of mycorrhizal fungi (II), whereas in aquatic ecosystems the CO_2 flux is mainly driven by physical forces such as convection affecting stratification (VII). The terrestrial carbon load, which is strongly controlled by precipitation (V, VII), also affects lake CO_2 efflux.

Besides CO_2, soils and lakes can emit CH_4. Anoxic condition can especially be found in soils saturated with water, but in aerated soils there can also be anaerobic niches (Sey et al. 2008). In the absence of oxygen, CO_2 can be used as an electron acceptor in respiration, and CH_4 is produced. In this study we found high CH_4 concentrations in soil. During the growing season, CH_4 concentrations increased more in the riparian zone than in the forest. In the riparian zone, soil can be saturated with water due to the proximity of the lake. High CH_4 production also reflects oxygen consumption through biological activity. The manual gas measurements at 50 cm depth showed that CO_2 concentrations were higher in the forest than in the riparian zone. Seasonal variation in the CH_4 concentration at 50 cm differed in the riparian zone from that in the forest. In the spring, the concentrations were of the same magnitude, but in course of the growing season the CH_4 concentration decreased in the forest but increased in the riparian zone; the soil in forest can be saturated with water at the time of snowmelt and dry during the summer, while the riparian zone is constantly under the influence of the lake. The peat layer may also be thicker in the riparian zone, which can increase CH_4 production, but our measurement points in the riparian zone as well as in the forest were peaty. The produced CH_4 is largely oxidised by methanotrophic microbes on its way to surface (Striegl & Michmerhuizen 1998, Kip et al. 2010), and the fluxes to the atmosphere can therefore be much smaller than would be anticipated on the basis of concentrations in the soil or water. In Valkea-Kotinen, CH_4 concentrations close to the soil surface were also similar to atmospheric concentrations.

Similarly to the deep soil layer, the hypolimnion of lakes can be anoxic during summer stratification and during the ice cover period. In Valkea-Kotinen, 80% of the CH_4 produced in sediments was oxidised in the water column and the annual CH_4 flux was 1.3 g C m^{-2} yr^{-1} (Kankaala et al. 2006). Even though the CH_4 emissions from lakes can be important in terms of climate change, as the global warming potential of CH_4 is 25 times greater than that of CO_2 (Forster et al. 2007), the contribution of CH_4 to carbon fluxes and carbon cycling in general is minor (Bastviken et al. 2004, Huotari 2011).

Not all the carbon in the soil escapes to the atmosphere or accumulates in soil organic matter. Water flowing through soil layers has the potential to carry carbon compounds not only downwards but also towards aquatic ecosystems, hence the term lateral carbon transport. Freshwaters are important pathways of terrestrial carbon to the atmosphere, not only in the boreal zone (e.g. Algesten et al. 2003) but also in tropical regions (e.g. Richey et al. 2002). At the European scale, rivers transport 53 Tg C yr^{-1} and emit 90 Tg C yr^{-1} of CO_2 to the atmosphere (Ciais 2008). In northern latitudes, the majority of carbon transport is in the form of DOC (Ciais 2008) and the majority of degassing at the European scale occurs at northern latitudes. Algesten et al. (2003) estimated that 30–80% of the organic carbon of terrestrial origin entering lakes is emitted to the atmosphere. In our catchment, the lacustrine emission to the atmosphere corresponds to 70% and the brook transport to 20% of the terrestrial input.

Carbon transport from soils to adjacent water bodies is mainly controlled by the hydrological regime, i.e. the amount of precipitation, its distribution and the length of the period of snow cover and frozen soil (e.g. Ågren et al. 2010). The forest cover in general smooths out the effect of heavy rains by enhancing the infiltration capacity and increasing evapotranspiration (Buttle et al. 2005, Guillemette et al. 2005). The forest cover also lowers the particle load to water bodies, because roots bind soil, the canopy reduces the force of raindrops hitting the ground and the litter cover on the forest floor reduces surface runoff. Forests also affect the environmental conditions in nearby lakes and rivers (Subehi et al. 2009). For example, in Valkea-Kotinen the tall forest shelters the lake from strong winds, and instead of wind action, the lake is prone to convection, i.e. the heat flux determines the degree of stratification (Nordbo et al. 2011). Trees in the riparian zone also cover the small stream, reducing its temperature compared to open areas. Small lakes such as Valkea-Kotinen are very abundant in the boreal zone, and lakes must therefore be studied in the context of forest ecology.

As a consequence of lateral carbon flux, the DOC concentration in Valkea-Kotinen brook was positively correlated with the amount of precipitation and DOC concentrations in the riparian zone (VI). This highlights the importance of the riparian zone as a carbon source, especially in the brook. In the lake, the large water volume buffered the system and changes were consequently not so easily detected. The close connection between the riparian soil and the brook was also observed in CO_2 concentration changes following rain events (V). The effect of the riparian zone on the DOC and DIC concentrations in the brook water increased downstream, and the buffering effect of the lake disappeared within less than 150 m downstream from the lake (V, VI). The rain-induced changes in the Valkea-Kotinen catchment are in agreement with findings in other boreal streams and lakes (e.g. Rantakari & Kortelainen 2005, Köhler et al. 2008).

The lake was an atmospheric source of carbon, apart from short periods in the summer, and acted as a pathway of terrestrially assimilated carbon into the atmosphere, as observed in many previous studies (e.g. Cole et al. 1994, Algesten et al. 2003, Sobek et al. 2006). This, together with the knowledge of net heterotrophy prevailing in the lake, is evidence of the utilization of allochthonous carbon (VII). The emissions from the lake were best explained by the surface water CO_2 concentrations. The CO_2 concentrations in the brook were related to concentrations in the soil and thus the terrestrial input (VI), whereas in the lake the stability of stratification affected the CO_2 concentration (VII). The stability of stratification decreased following the cooling of air and the often simultaneous rainfall and higher wind. However, the terrestrial input after heavy rain events could also result in CO_2 bursts (VII). Probably due to the large water volume in the lake, the effects of smaller rain events were not visible, although they were observed in the brook.

The terrestrial carbon input is indispensable for the functioning of aquatic food webs. Allochthonous terrestrial carbon can account for 95% of the total carbon input to a lake and

80% of CO_2 emissions (Jonsson et al. 2001). In Lake Valkea-Kotinen, the average annual primary production is 31 g C m^{-2} yr^{-1} (Keskitalo et al. 1998), i.e. much higher than in boreal lakes in general (Algesten et al. 2003). Taking into account the primary production and input from precipitation (1.6 g C m^{-2} yr^{-1}), the terrestrial input (DOC+DIC) forms 76% of the total carbon input in Valkea-Kotinen. For lakes in other regions besides the boreal zone, the importance of terrestrial carbon can be smaller, because their own autochthonous production is higher (Stenuite et al. 2009).

In Valkea-Kotinen, roughly 90% of the terrestrial export is in the form of DOC and 10% is DIC. In contrast, Kindler et al. (2011) observed that DIC leaching exceeded DOC leaching, and estimated that the leaching of biogenic DIC and DOC was 8.3 ± 4.9 g m^{-2} yr^{-1} and 3.5 ± 1.3 g m^{-2} yr^{-1}, respectively, for forests. However, in acidic topsoils (cf. average soil water pH 3.8 at Valkea-Kotinen), DIC leaching represented <10% of the total carbon leaching. Buffam et al. (2011) also observed that the proportion of DOC in total carbon export was higher in wetlands than in forests, which is in accordance with our results, since the peat layer around Lake Valkea-Kotinen and its brook is thick. Kindler et al. (2011) also noted that there is large variation in carbon leaching between sites of the same land-use type, and the result from Valkea-Kotinen (Fig. 8) corresponds well with the overall average of 19 (or median 15 g m^{-2} yr^{-1}) and with the wetland runoff values (11 and 0.6 g C m^{-2} yr^{-1} for DOC and DIC, respectively) reported by Buffam et al. (2011). According to Kindler et al. (2011), the net ecosystem carbon balances of forests were little affected by leaching. However, leaching losses can be much more important for agricultural carbon balances. Moreover, the carbon emission from lakes can be similar in magnitude to the net emissions from terrestrial ecosystems in northern Sweden (Karlsson et al. 2010). Buffam et al. (2011) estimated that the regional output of carbon by rivers in the Northern Highlands Lake District in North America accounted for 3% of the regional total NEE.

The average terrestrial NEE of the Valkea-Kotinen catchment (33 g C m^{-2} yr^{-1}) was low compared to other boreal forests (Kolari et al. 2004, Lussyart et al. 2008), even though 2009 yielded comparable values (110 g C m^{-2} yr^{-1}). In Valkea-Kotinen, NEE has probably decreased from its maximum values, which often occurs in stands of medium age (Kolari et al. 2004), even though old-growth forests still sequestrate carbon (e.g. Luyssaert et al. 2007). Because of low NEE, the lateral carbon transport in Valkea-Kotinen is considerable, whereas in younger or managed forests its significance can be smaller. At the catchment scale in Valkea-Kotinen, the loss of carbon through export to the brook represented 17% of the catchment NEE (or 11% of the terrestrial NEE, or 30% of the aquatic NEE). In a northern Swedish forested catchment, lateral carbon transport accounted for only 6% of the terrestrial NEE (Jonsson et al. 2007). However, our results correspond with those of Dinsmore et al. (2010), which showed a peatland catchment losing 24% of NEE as DOC. Furthermore, in a Swedish mire complex the aquatic loss was 34% of the annual carbon uptake (Nilsson et al. 2008). The proportion of peatland in Valkea-Kotinen is over 20% and the lake shores are histosols, which can increase lateral transport compared with mineral soils. The proportion of peatlands in a catchment is known to control the DOC concentration in lakes and outflowing streams (e.g. Kortelainen et al. 2006).

Even though the riparian zone is the link between terrestrial and aquatic ecosystems, the whole catchment affects the lateral carbon transport. The riparian zone mainly determines the amount of carbon that is prone to be transported, whereas the whole catchment affects the water flows transporting the carbon. In the ^{14}C-labelling experiment, only a minor fraction of the assimilated carbon was found free in the soil solution (II). This indicates that the carbon is effectively used by microorganisms, producing CO_2, or bound to organic or mineral particles. The small amount of free carbon in soil solutions also indicates that free carbon does not move long distances. This emphasizes the role of the riparian zone as a source of DOC in lakes and streams, since during the transport from deeper forests carbon is either respired or adsorbed before it enters water bodies. Isotopic studies have also demonstrated that most of the carbon entering streams is young (Raymond et al. 2007).

Most water bodies are fed by water from the soil, either as surface flow or as percolation through soil layers, and water thus also transports carbon compounds to lakes and streams. In areas where evapotranspiration exceeds precipitation, there is no such water flow and the loss of terrestrial carbon through water transport can therefore be negligible. However, in the boreal zone the leakage of carbon from the terrestrial ecosystem is important. Huotari et al. (2011, VII) stated that CO_2 emission from the lake corresponds to 10% of terrestrial net ecosystem production and would thus reduce the role of forests as a carbon sink by 10%. The study (VII) only considered carbon export from the lake to the atmosphere, and the inclusion of DOC export via the outflowing brook and modelling of the NEE of this particular forest would reduce the role of the forest as a carbon sink even further. This study demonstrated that lateral carbon transport from soils to fresh waters could even amount to 50% of the terrestrial NEE of old-growth forests, and lake CO_2 emissions could represent 37% of it. Based on these findings, it can be stated that natural inland waters are an integral part of terrestrial carbon cycling and should thus be taken into account in balance and budget calculations and when considering the strength of regional as well as global terrestrial carbon sinks (Hope et al. 2001, Luyssaert et al. 2007, Battin et al. 2008). At the global scale, the role of boreal forests as carbon sinks is overestimated if the lateral carbon flux to aquatic ecosystems is ignored.

Climate change, with increasing temperatures and a changing precipitation regime, will alter the components of the carbon cycle in northern latitudes, because temperature and water availability affect several biological processes, including photosynthesis and respiration. Higher soil temperatures increased photosynthesis, soil respiration as well as shoot, root and rhizosphere respiration of silver birch, Norway spruce and Scots pine seedlings (I, II, III). However, in drier boreal soils a temperature increase does not always increase decomposition (Allison & Treseder 2008). In our study, the net CO_2 exchange did not change significantly with increasing temperature due to the simultaneous increase in photosynthesis as well as in respiration (I). Although temperature itself affects the rate of respiration, increased photosynthesis can further accelerate it through the input of recently assimilated carbohydrates as rhizodeposition and root exudates (I). Photosynthesis and respiration were more sensitive to a temperature change from cold (7–12 °C) to medium (12–15 °C) temperatures than from medium to warm (16–22 °C) temperatures. The increased temperature did not change the species composition of ectomycorrhizal fungi (I). However, for Scots pine, the increased temperature reduced the percentage of mycorrhization (II). Even though our results suggest that warming does not increase biomass accumulation or belowground respiration in these boreal species in southern Finland, a similar temperature increase at northern latitudes would probably increase the turnover rate of assimilated carbon. Faster decomposition releases nitrogen, which is often the nutrient limiting growth. An increased amount of available nitrogen together with higher temperatures could enhance the accumulation of carbon in seedling biomass.

A higher temperature and precipitation could increase lateral carbon transport, because the hydrological regime largely controls carbon transport. Temperature-dependent decomposition can produce more easily soluble organic compounds prone to lateral transport, and higher precipitation increases the water flow from soil to water bodies.

Climate change will also affect the stability of stratification in lakes, which in humic water bodies means that summer stratification will become stronger. However, the role of convection will probably increase and autumn mixing periods could become longer. Thus, warmer autumns will enhance the role of autumns in the annual carbon flux. This is already clear in terrestrial ecosystems (Piao et al. 2008, Vesala et al. 2010). Climate change could also increase the frequency of extreme weather events, which are important for lateral carbon transport. The effect of rain on DIC concentrations in the brook was clearly observed in our study (V). Abundant rains can also influence the DOC concentrations of lakes (VII, Ojala et al. 2011).

A higher temperature could enhance photosynthesis, increasing the water requirements of vegetation, which will then reduce lateral water flow. A higher temperature could also increase evapotranspiration, which will additionally reduce the lateral water flow. Thus, even though more carbon might be available for lateral transport, there will be less water to carry it. On the other hand, an increased CO_2 concentration in the atmosphere would reduce the water consumption in photosynthesis by higher plants, which could increase the lateral water flow and thus lateral carbon transport.

CONCLUSIONS

The processes contributing to the carbon cycle are important for understanding and modelling the carbon balance. This is especially important under the changing climate and when estimating carbon emissions at the landscape level. In this study, I combined carbon cycle measurements at different scales to gain information on carbon cycling in the boreal zone. Microcosm measurements revealed differences between tree species in their responses to increasing temperatures, and that ectomycorrhizal fungi can have a significant effect on the carbon balance. Both long-term biomass accumulation and short-term ^{14}C labelling demonstrated that a higher temperature did not change the net growth of tree seedlings, because both photosynthesis and respiration increased, compensating for each other.

At the landscape level, terrestrial and aquatic ecosystems are closely linked and DOC and DIC fluxes from the riparian soil in the Valkea-Kotinen catchment largely determined the concentrations in the adjacent brook. From the terrestrial perspective, the amount of carbon that is transported to aquatic environments is small compared with direct fluxes between the atmosphere and forests, but considerable if compared with NEE. The significance of transported carbon for the growth of forest vegetation or decomposition in the soil is probably minor, but it is important to also consider this part of the carbon cycle when calculating the carbon balance of a terrestrial ecosystem. The terrestrial export of carbon from soils to water bodies can account for 50% of forest NEE, and the role of terrestrial ecosystems as carbon sinks could therefore be largely overestimated if lateral carbon fluxes are excluded. The annual variation in temperature-controlled respiration was higher than in photosynthesis, which leads to large variation in terrestrial NEE. However, the annual variation in DOC and DIC concentrations in the soil were small and lateral carbon fluxes were mainly controlled by hydrology. Nevertheless climate change could cause long-term changes in photosynthesis, respiration and decomposition, which will affect the availability of soil carbon for lateral transport.

In this study, water fluxes were considered at the catchment scale, but it would be fruitful to investigate the pathways of water more carefully in order to understand which carbon stores in the soil are most prone to lateral transport. The quality and concentration of carbon in the soil vary significantly, and the pathways can thus determine the properties of carbon entering lakes and streams. As boreal lakes often depend on terrestrial carbon inputs, changes in their quantity and quality could have significant effects on aquatic carbon cycling.

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