Carbon balance and component CO$_2$ fluxes in boreal Scots pine stands

Pasi Kolari

Department of Biological and Environmental Sciences
Faculty of Biosciences
University of Helsinki

Academic dissertation

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ABSTRACT

This study quantifies and analyses the dynamics of carbon balance and component carbon dioxide (CO$_2$) fluxes in four Southern Finnish Scots pine stands that covered the typical economic rotation time of 80 years. The study was based on direct flux measurements with chambers and eddy covariance (EC), and modelling of component CO$_2$ fluxes.

The annual CO$_2$ balance varied from a source of about 400 g C m^{-2} a^{-1} at a recently clearcut site to net CO$_2$ uptake of 200–300 g C m^{-2} a^{-1} in a middle-aged and a mature stand. A 12-year-old sapling site was at the turning point from source to a sink of CO$_2$. In the middle-aged stand, photosynthetic production was dominated by trees. Under closed pine canopies, ground vegetation accounted for 10–20% of stand photosynthesis whereas at the open sites the proportion and also the absolute photosynthesis of ground vegetation was much higher. The aboveground respiration was dominated by tree foliage which accounted for one third of the ecosystem respiration. Rate of wood respiration was in the order of 10% of total ecosystem respiration. CO$_2$ efflux from the soil dominated the ecosystem respiratory fluxes in all phases of stand development.

Instantaneous and delayed responses to the environmental driving factors could predict well within-year variability in photosynthetic production: In the short term and during the growing season photosynthesis follows primarily light while the seasonal variation is more strongly connected to temperature. The temperature relationship of the annual cycle of photosynthesis was found to be almost equal in the southern boreal zone and at the timberline in the northern boreal zone. The respiratory fluxes showed instantaneous and seasonal temperature relationships but they could also be connected to photosynthesis at an annual timescale.

Keywords: photosynthesis, respiration, chamber, eddy covariance, modelling

ACKNOWLEDGMENTS

LIST OF ORIGINAL ARTICLES

The thesis is based on the following research articles, which are referred to in the text by their Roman numerals:

I   Kolari, P., Pumpanen, J., Rannik, Ü., Ilvesniemi, H., Hari, P. & Berninger, F. 2004. Carbon balance of different aged Scots pine forests in Southern Finland. Global Change Biology 10: 1106–1119.

II   Kolari, P., Lappalainen, H.K., Hänninen, H. & Hari, P. 2007. Relationship between temperature and the seasonal course of photosynthesis in Scots pine at northern timberline and in southern boreal zone. Tellus 59B: 542–552.

III   Mäkelä, A., Kolari, P., Karimäki, J., Nikinmaa, E., Perämäki, M. & Hari, P. 2006. Modelling five years of weather-driven variation of GPP in a boreal forest. Agricultural and Forest Meterology 139: 382–398.

IV   Kolari, P., Pumpanen, J., Kulmala, L., Ilvesniemi, H., Nikinmaa, E., Grönholm, T. & Hari, P. 2006. Forest floor vegetation plays an important role in photosynthetic production of boreal forests. Forest Ecology and Management 221: 241–248.

V   Kolari, P., Kulmala, L., Pumpanen, J., Launiainen, S., Ilvesniemi, H., Hari, P. & Nikinmaa, E. 2009. CO_2 exchange and component CO_2 fluxes of a boreal Scots pine forest. Boreal Environment Research 14: 761–783.

Author's contribution:
Pasi Kolari participated in planning of the research and in conducting the measurements, made the data analyses and was the main author in papers I, II, IV and V. In paper III, Pasi Kolari analysed the experimental data that was utilised in the stand photosynthesis model and participated in the model development and writing of the article. Paper II will also be included in the PhD thesis of Hanna Lappalainen.

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INTRODUCTION

The boreal coniferous forests are the most widely distributed vegetation type in the world covering 19% of the earth land surface (FAO 2000). Boreal forest soils are among the largest terrestrial carbon pools, estimated to contain approximately 15% of the soil carbon (C) storage worldwide (Schlesinger 1977, Post et al. 1982). The role of the boreal forests in the global carbon cycle is thus significant. The forests take up carbon dioxide (CO_2) from the atmosphere, store carbon as organic macromolecules in biomass and release CO_2 through oxidative processes in the living biomass. Quantification of the present carbon balance of forests is essential in assessing the role of forests in the global carbon cycle. Identifying and understanding the processes behind the observed net carbon balance is also necessary for being able to predict the carbon balance of forest ecosystems in changing climate.

Before the wider adoption of micrometeorological methods in the 1990's, large-scale carbon balance studies were mostly based on combining inventories of tree biomass and satellite images (Kauppi et al. 1992, Dixon et al. 1994, Myneni et al. 2001, Nabuurs et al. 2003). Forest inventories suggest a long-term average sink of 70 g C m^{-2} a^{-1} in European forests (Janssens et al. 2003). Similar estimations of the continental carbon balance have been obtained with inversion modelling, i.e. deriving the C balance from the records of atmospheric CO_2 concentration (e.g. Keeling et al. 1996, Bousquet et al. 1999). The uncertainty in the obtained results, however, is large; approximately 50% of the estimated sink (Stephens et al. 2007).

Exchange of CO_2 between a forest ecosystem and the atmosphere can be determined directly by micrometeorological method called eddy correlation or eddy covariance (EC). The eddy-covariance measurement does not disturb the ecosystem being studied and the instrumentation requires relatively little maintenance, therefore eddy covariance is an ideal method to measure ecosystem gas exchange continuously over extended periods. With the technical development, increasing availability and more affordable prices of fast-responding digital measuring devices and data acquisition instrumentation, eddy covariance rapidly gained popularity in the 1990's (Baldocchi 2003). Recent studies on forest ecosystem carbon balance have mainly been based on long-term measurements of net CO_2 exchange of the ecosystem by eddy covariance. The measured fluxes have been used for analysing the relationships between CO_2 exchange of boreal forests and climatic factors (e.g. Suni et al. 2003a, Wang et al. 2004, Lagergren et al. 2008) and for inspecting the variability of ecosystem carbon balance across geographical gradients (e.g. Luyssaert et al. 2007a, Magnani et al. 2007). Data from eddy covariance is also nowadays probably the most frequently used material for developing and testing models of land ecosystem carbon cycle (e.g. Knorr and Kattge 2005).

Eddy-covariance measurements in temperate and boreal forests initially indicated that forests were strong sinks of carbon (e.g. Valentini et al. 2000, Aubinet et al. 2001). Flux-based estimates of the C sink in the forests in EU varied from 0.17–0.35 Gt C a^{-1} (Martin et al. 1998) to 0.47 Gt C a^{-1} or 185 g C m^{-2} a^{-1} (Papale and Valentini 2003). However, measurements in late 1990's and early 2000's were mainly conducted in middle-aged forests that were close to their peak rates of biomass accumulation rather than representing the C balance of a landscape consisting of forest stands at different phases of their life cycles (Black et al. 2005). The great majority of forests are subject to developmental cycles that are initiated by forest management or natural disturbances like storms or fires (Geider et al.

2002). Large amounts of organic carbon are returned to the atmosphere during and after disturbances. Therefore, estimating the C balance of forests during their whole life cycle also required measurements at disturbed sites. Joint European project Carbo-Age (paper I) that aimed to assess the age-related changes in forest carbon balance was conducted in 2000–2002. The cumulative carbon sequestration over the rotation time in the studied forests was found to be approximately half of the peak C sequestration (Magnani et al. 2007), implying European forest sink of approximately 90 g C m^{-2} a^{-1}.

Another way to study CO_2 exchange between a forest ecosystem and the atmosphere can be also be studied using a "bottom-up" approach where the component fluxes are separately determined. The net gas exchange consists of an aggregation of small-scale phenomena that can be traced down and studied separately. The more detailed insight into different processes can be used in explaining or predicting ecosystem-level observations. Integration of component CO_2 fluxes will produce alternative estimates of ecosystem CO_2 exchange as well as help us understand the significance of different processes in the carbon balance. The observed variability in photosynthetic CO_2 uptake among different forest stands can be explained by climatic factors (light, temperature, length of growing season), soil properties (fertility, water availability or retention capacity), and stand structure and physiology (the amount of photosynthesizing foliage or light interception by the foliage, and photosynthetic capacity). Age-related changes in CO_2 exchange result from changes in stand and tree structure and decomposable carbon pools rather than the stand age itself.

Upscaling of fluxes to the stand level requires idealising and simplifying assumptions on the spatial variation of the environmental driving factors and on the physiological properties of different functional compartments. Uncertainties in the component fluxes and driving factors accumulate in the integration. The net CO_2 exchange of a forest ecosystem results from relatively small difference between two large fluxes of opposite sign: photosynthesis and respiration. The uncertainty in the integrated carbon balance can be large compared to the uncertainty of a direct measurement of net ecosystem CO_2 exchange. Therefore, it is beneficial to employ both integration of process-based small-scale CO_2 flux estimates and direct stand-scale observations of CO_2 exchange that circumvent the intermediate steps involved in the integration.

Aim

This study aims to quantify the CO_2 balance and its component fluxes in boreal Scots pine forest ecosystems. The regular patterns of the CO_2 exchange, connections to the stand structure, and the environmental responses of the component CO_2 fluxes are identified to explain the instantaneous and cumulative CO_2 exchange in the studied forest stands. Because biomass accumulation and the rates of the CO_2-releasing processes in the long term depend on the amount of carbon fixed in photosynthesis, analysis of the spatial and temporal variation of photosynthetic rate is emphasized.

The specific objectives of the studies were
   - to assess the carbon sink strength of selected different aged Southern Finnish Scots pine stands and the partitioning of CO_2 fluxes into photosynthesis, autotrophic respiration and decomposition of organic matter within the stands (paper I)

- to determine the relationship between temperature and the annual cycle of photosynthesis in Scots pine (paper II)
- to quantify the photosynthetic production of trees in a forest ecosystem and test models of stand photosynthesis (paper III)
- to quantify the photosynthetic production of the ground vegetation in a forest ecosystem (paper IV)
- to assess the partitioning of the net CO_2 exchange of a Scots pine stand into component CO_2 fluxes: photosynthesis of trees and ground vegetation, respiration of foliage, stems and CO_2 efflux from the ground (paper V)

This study combines two approaches for quantifying the ecosystem CO_2 exchange. First, direct measurements of CO_2 fluxes are utilised to determine the ecosystem CO_2 balance in stands of different ages (papers I and V). Secondly, the component CO_2 exchange processes are analysed separately using measured CO_2 fluxes and modelling. The annual cycle of photosynthesis on the shoot scale was studied in paper II. In papers III and IV, the instantaneous photosynthetic rate at a small scale was integrated over space and time using models for spatial variation of light environment and the annual cycle of photosynthesis. In paper V, also respiration components were quantified and their annual cycles analysed. The component fluxes were combined to determine the net carbon balance of a middle-aged pine stand.

PROCESSES BEHIND ECOSYSTEM CARBON DIOXIDE EXCHANGE

The exchange of carbon dioxide in a forest ecosystem is generated by processes binding CO_2 from the atmosphere and processes that release CO_2. Photosynthesis is the fundamental carbon-binding process and the ultimate origin of all organic carbon accumulated in land ecosystems. Photosynthetic products are either used directly for the metabolism of photosynthesizing tissues or transported to other parts of the plant where they are used for formation and growth of new tissues or the chemical energy bound in photosynthates is utilised for maintenance of cell metabolism. CO_2 is released in the respiratory processes involved in maintenance and growth. Figure 1 summarises the carbon flows in a forest ecosystem.

Plants accumulate carbon as biomass during their life cycle but also produce litter in form of bark fragments, falling leaves and branches, and dead fine roots. At stand level, mortality due to excessive plant density (self-thinning) or external factors (cutting, storms, fire, diseases) also produces woody debris. Eventually the carbon bound in plant biomass will be released as CO_2 through decomposition of dead biomass. The rates of the processes that accumulate carbon (photosynthesis and growth) and the residence time of carbon in the living and dead biomass determine the overall carbon balance of the forest ecosystem.
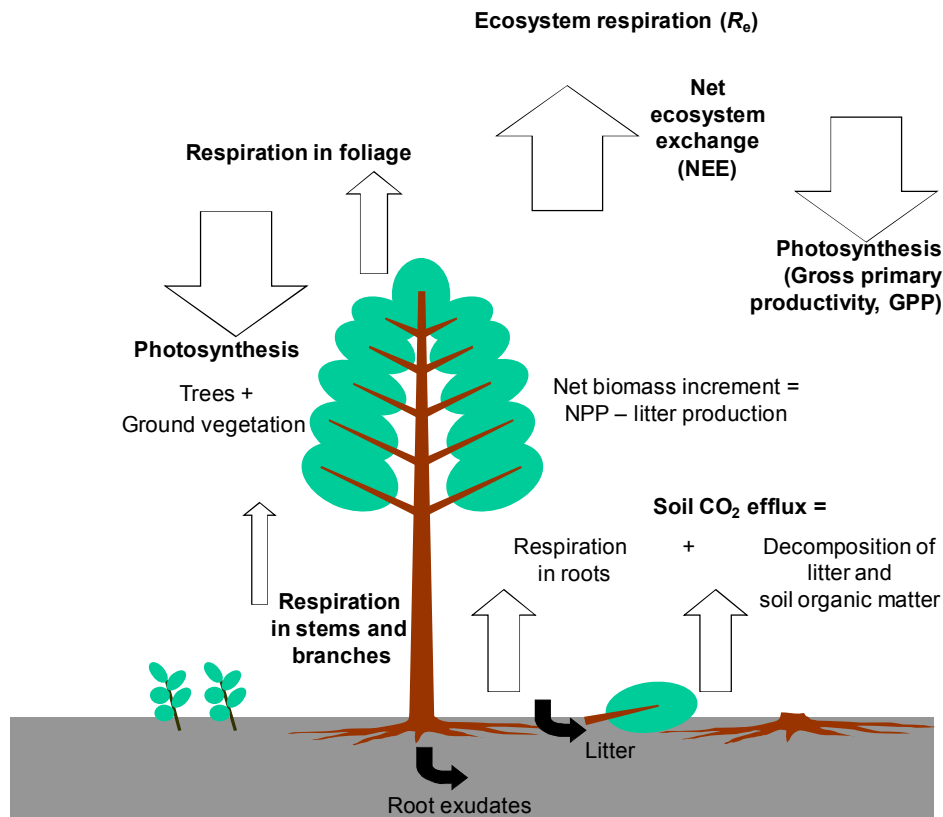
Figure 1. Carbon flows and storage in a forest ecosystem. Uptake of CO_2 is indicated by downward arrows, release of CO_2 by upward arrows. Black arrows denote carbon flows within the forest ecosystem. Items labelled in **bold** face indicate the fluxes that this study particularly addressed.

Photosynthesis

Photosynthesis takes place in chloroplasts in the mesophyll cells of leaves. There are two main reaction chains in photosynthesis. The light reactions occurring in thylakoids of chloroplasts convert solar radiation energy into chemical form; in addition, water is split and oxygen is released. Fixation of CO_2, also called "dark reactions" or "carbon reactions", takes place in chloroplast stroma utilising the energy bound in the light reactions.

The driving factors of photosynthesis in short term are relatively well understood (Farquhar and von Caemmerer 1982). The availability of light energy often limits the photosynthetic rate. At low light, the photosynthetic rate increases almost linearly with photon flux density (Figure 2). The difference between the ambient CO_2 concentration and mesophyll CO_2 drives diffusion of CO_2 into the leaf. Photosynthetic rate is in turn dependent on the availability of CO_2, i.e. the internal CO_2 concentration in the leaf mesophyll. The rate of
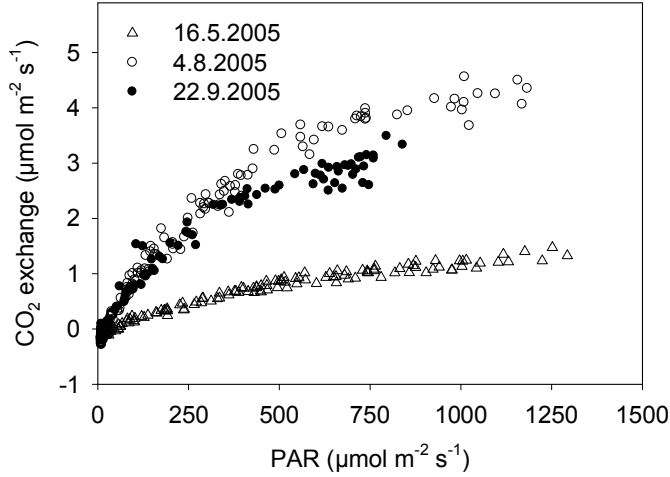
Figure 2. Relationship between photosynthetically active radiation (PAR) and pine shoot CO_2 exchange at SMEAR I in Värriö, Lapland, on three days in spring, summer and autumn (paper II).

CO_2 fixation is also related to temperature through the temperature responses of the biochemical reactions and transport of CO_2 into and inside the leaf (e.g. Wullschleger 1993, Bernacchi et al. 2002).

Diffusion of CO_2 into plant leaves is controlled by the stomata that simultaneously limit loss of water from the plant. The function of stomata has been described empirically as a response to evaporative demand and radiation and as a feedback from photosynthesis to maintain leaf internal CO_2 (e.g. Ball et al. 1987, Leuning et al. 1995) or theoretically applying the principle of plants maximising CO_2 uptake minus transpiration cost (Hari et al. 1986). The availability of plant extractable water in soil explains well the stomatal action under drought (Federer 1979, Duursma et al. 2008).

Models of photosynthesis range from simple saturating light response functions to detailed biochemical models (Farquhar and von Caemmerer 1982) and dynamic models (e.g. Kirschbaum et al. 1998). The model used in this study is the optimal stomatal control model (Hari et al. 1986). The model comprises the following equations for photosynthesis A, dark respiration R and stomatal conductance g_s as functions of ambient CO_2 concentration C_a, saturation deficit of water vapour at leaf surface D and leaf temperature T_l:

$$A = C_i f(I) = \frac{(g_s C_a + R) f(I)}{g_s + f(I)} \tag{1}$$

$$R = Max\left(0, r_0 Q_{10}^{T_l/10} + r_1\right) \tag{2}$$

$$g_s = \left(\sqrt{\frac{C_a - R(T_l)/f(I)}{1.6 \lambda D}} - 1\right) f(I) \tag{3}$$

Stomatal conductance g_s is limited between the cuticular conductance g_{min} and conductance when the stomata are fully open, g_{max}. 1.6 is the ratio of diffusivity of water vapour relative to diffusivity of CO_2. The parameter λ is the cost of transpiration, i.e. the carbon required in the long term to sustain transpiration flow. It can also be considered as a measure of water-use efficiency. The function $f(I)$ represents the light response of the biochemical reactions of photosynthesis as

$$f(I) = \frac{\beta I}{I + \gamma} \tag{4}$$

Parameter γ is the curvature of the light response. It also gives the relationship between the light-saturated value and the initial slope of $f(I)$. The initial slope of $f(I)$ describes the efficiency of photochemistry, i.e. light harvesting in the chloroplasts (quantum yield per unit internal CO_2 concentration). The key parameter in the annual variation of photosynthesis is photosynthetic efficiency β, which is equivalent to the maximum rate of carboxylation. When multiplied by the intercellular CO_2 concentration in the leaf (eq.1) it equals to the rate of light-saturated photosynthesis.

The instantaneous responses of photosynthetic rate to the environmental driving factors vary over seasons due to changes in the state of the photosynthetic machinery (Figure 2). In winter, full dormancy is obvious in deciduous trees but the evergreen conifers often retain the ability to photosynthesize, even though at low rate, when the momentary conditions are favourable (e.g. Ensminger et al. 2004). Especially in early spring when intense light exposure of foliage is combined with low temperatures the light reactions are downregulated and the excess light energy dissipated as fluorescent radiation and heat (Öquist and Huner 2003, Porcar-Castell 2005). The subprocesses of photosynthesis are dependent on each other (Schulze et al. 1994); the conversion of light energy to intermediate chemical compounds such as adenosine triphosphate (ATP) must match the consumption of the energy in carbon fixation. Therefore, the curvature of the light response $f(I)$ in Scots pine remains similar throughout the year although the level varies. Thus, the state of the photosynthetic machinery as a whole can be described with just one parameter, photosynthetic efficiency β that increases in spring, levels off for the summer, and declines again in autumn (Hari and Mäkelä 2003, paper II).

In boreal evergreen conifers, photosynthetic capacity (maximum light-saturated photosynthesis) is not pre-determined to grow monotonically in the spring, but during cold spells it can also decrease (Polster and Fuchs 1963, Pelkonen 1980). The seasonal cycle of photosynthetic capacity can be described as a slow acclimation to prevailing temperature (Pelkonen and Hari 1980, Mäkelä et al. 2004, paper II). The delayed effect of temperature is described by a theoretical variable, state of acclimation (S) that corresponds to the temperature the photosynthetic apparatus is acclimated to:

$$\frac{dS}{dT} = \frac{T_1 - S}{\tau} \tag{5}$$

where T_1 is leaf temperature and τ a time constant, i.e. the slowness of the acclimation of the photosynthetic apparatus. Photosynthetic efficiency β is related to S through linear (Mäkelä et al. 2004) or sigmoid (paper II) relationship. The value of β is further modified by an instantaneous temperature response and short-term carry-over effects of freezing

temperatures (paper II). The role of temperature acclimation in the annual cycle varies geographically; it is obvious in the boreal zone whereas in regions of milder climate other factors such as water availability are also important (Reichstein et al. 2007, Mäkelä et al. 2008).

Photosynthesis in trees has been studied extensively. Carbon dioxide exchange of ground vegetation, however, is less well known. Excluding the early phases of stand development, the forest floor is shaded by trees. Thus it is reasonable to expect that the light response of photosynthesis in the ground vegetation is such that low light is efficiently utilised but photosynthesis saturates at fairly low irradiances. In the boreal zone, the ground vegetation is covered by snow in winter. According to Starr and Oberbauer (2003), however, evergreen ground vegetation species can fix some carbon under snow cover. Another special feature is the abundance of mosses that have different physiology from the vascular plants; for instance, water status of mosses varies rapidly which is reflected in photosynthesis and respiration (Skre and Oechel 1983, Kulmala et al. 2008).

Autotrophic respiration

The energy for biosynthesis of new molecules or transport through membranes is taken from oxidation of energy-rich carbon molecules, such as sugars, and stored in intermediate compounds such as ATP. This process, called respiration, produces many important carbon precursors for cellular metabolism, and releases CO_2. Traditionally, a distinction is made between maintenance and growth respiration (Thornley 1970) although the biochemical processes in both are similar. For instance, leaf respiration has been related to maintenance of enzymes and pigments that determine the photosynthetic capacity (Ryan 1995). The proportion of photosynthates utilised for maintenance respiration locally in leaves is in the order of 20–30% annually (Ryan et al. 1997a). At whole-plant level, respiration is also constrained by the supply of sugars produced in photosynthesis. Over longer time periods, tree- and stand-level respiration is suggested to be proportional to photosynthetic production of leaves (Dewar et al. 1998, Waring et al. 1998). Root growth and supply of root exudates into the soil, thus influencing the soil CO_2 efflux, are also related to photosynthetic production (Pumpanen et al. 2008).

Production of CO_2 is proportional to the amount of sugars used up and chemical energy released in respiration, therefore, CO_2 efflux from the respiring tissues is taken as the rate of respiration. In photosynthesizing leaves, night-time CO_2 exchange directly gives the rate of dark respiration in leaves, but respiration in light must be determined indirectly. This is normally done by determining the regression of night-time fluxes on temperature and extrapolating that regression to daytime. The leaf respiration in light has been suggested to be considerably smaller than in the dark, although exact measurements are difficult to obtain (e.g. Hoefnagel et al. 1998, Pinelli and Loreto 2003). In some cases, for instance in tree stems, the transport of CO_2 out of the respiring tissues must be considered when interpreting the observed CO_2 effluxes; there is delay between the CO_2 production and the observed efflux. Part of the CO_2 respired by the stem tissues is also transported upwards in xylem sap (Teskey et al. 2008). Therefore, vertical profile of CO_2 efflux varies depending on transpiration rate (Hölttä and Kolari 2009).

Strong dependence on temperature is characteristic for enzymatic reactions, and rate of respiration in plant tissues is often described as an exponential function of temperature (e.g. Lloyd and Taylor 1994). Like photosynthesis, also the respiration components follow an

annual cycle (paper V). Seasonal variation in respiration has been traditionally explained by the temperature of the respiring tissues or their surroundings. Thus respiration of the aboveground tissues shows similar seasonal course as air temperature (Zha et al. 2003, 2005). The seasonal course of soil CO_2 efflux can often be explained well by soil temperature (Davidson et al. 1998). In some cases also year-to-year variation can be explained by differences in soil temperature during the growing season (Zha et al. 2007). The observed temperature relationships should, however, be considered as merely apparent response because the processes and the driving factors behind the observed CO_2 effluxes are more complicated and not yet fully understood. For example, the separation of root respiration from the total CO_2 efflux from the ground is problematic (Ryan and Law 2005). Methods like excision of roots (trench plots) or girdling of the trees can be employed to separate the respiration components (Hanson et al. 2000) but the strong connection between root respiration and the supply of easily decomposable organic compounds, root exudates, into the vicinity of the roots complicates interpretation of those experiments (Subke et al. 2006, Trumbore 2006).

Decomposition of biomass

New biomass is formed using the sugars produced in photosynthesis. The raw material is allocated to formation of photosynthesizing tissue (foliage), water-conducting and supporting tissues (wood and coarse roots) and tissues enabling water and nutrient uptake (fine roots).

Residence time of carbon in trees varies. A large part of the carbon bound in photosynthesis is promptly used for maintenance or released as root exudates that feed the microbes in the rhizosphere. Some of the sugars are stored as starch to be used in the near future. The rest of the carbon is used for construction of plant structures; the amount of new tissues formed is called net primary production (NPP). Carbon in the foliage of a tree has life time of couple of months to several years depending on the longevity of the leaves. The woody structures that are mostly made of cellulose and lignin comprise the most stable storage of carbon.

Trees shed senescing leaves and fine roots, pieces of bark and dead branches as litter. At stand level, forest management and mortality due to excessive plant density (self-thinning) or external factors (storms, fire, diseases) further produces woody debris. The composition of dead biomass varies during the life cycle of a forest stand. There is steady annual input of litter that is related to the standing biomass and the annual growth. Disturbances like cutting or storms introduce additional woody debris in form of detached branches and stems lying on the ground, as well as abandoned stumps and roots. The organic macromolecules that comprise the biomass are enzymatically broken down and utilised by soil organisms. The soil microbes function in soil solution and use extracellular enzymes to decompose soil organic matter. Microbial metabolism releases CO_2 into the soil (heterotrophic respiration) and thus returns the carbon assimilated by the plants back into the atmosphere. Decomposition products too large to be taken up by microbes produce decay-resistant organic matter, humus. The lifetime of humus is very long, on the scale of millennia (Liski et al. 2005).

Major factors affecting microbial respiration in the soil are the amount and quality of organic carbon in the soil, soil temperature and soil moisture (Kirschbaum 1995, Davidson et al. 1998, Prescott et al. 2004). The rate of decomposition is related to temperature in an

exponential fashion (Lloyd and Taylor 1994). Numerous studies have shown the relationship between soil moisture and microbial activity (e.g. Davidson et al. 1998, Pumpanen et al. 2003). Decomposition slows down in drying soil and eventually the microbes themselves may be affected by the drought through desiccation. The rate of decomposition in a forest stand naturally also depends on the amount and quality of the substrate available. Gershenson et al. (2009) found that increased substrate availability also increased the temperature sensitivity of soil CO_2 efflux, which suggests that decomposition in the soil is substrate-limited and increase in temperature does not necessarily lead to exponential increase in the rate of decomposition.

Relationships between stand age, stand structure and CO_2 exchange

Short-term variability in stand CO_2 exchange mainly results from instantaneous responses of CO_2 exchange processes, photosynthesis and respiration, to the driving factors such as light and temperature (Medlyn et al. 2003, paper III). The instantaneous responses vary seasonally due to seasonal changes in the physiological activity in plants and soil organisms (annual cycle). In the long term, over the course of the trees' lifespan, the relationships between the environment and CO_2 exchange become more strongly connected to stand structure due to development of the individual trees and their arrangement in the stand. In managed forests the natural succession is further altered by silvicultural measures. Changes in the sizes of different biomass compartments and the allocation of carbon during stand development modify the distribution of CO_2 sources and sinks in the stand. The amount of supporting and water-conducting structures (coarse roots, stem and branches) increases during tree growth, whereas foliage biomass saturates.

Plants modify the microclimate within the stand. The structure of the vegetation affects the partitioning of solar energy input into thermal radiation and fluxes of sensible and latent heat (Rannik et al. 2002). The environmental driving factors show spatial variability in a forest canopy. Light is the driving factor that has the strongest variation within the canopy (Norman 1980). Absorption and transmission of light in the canopy creates complex pattern of different light intensities; sunflecks and more or less shaded patches that also move in time (Figure 3).

Light conditions in different stands are strongly related to stand structure. In the open canopy of a young forest, the whole foliage receives ample sunlight whereas in a closed canopy leaves in the lower canopy are shaded by the upper canopy. Height of a tree in relation to other trees in the stand also determines its light environment. The seasonal variation in foliage area also affects photosynthetic production of a tree or stand via increasing shading in the existing foliage by the new leaves. Spatial variation in the prevailing light environment eventually leads to structural acclimation, differentiation of sun and shade leaves or shoots that have different morphology and orientation (Boardman 1977). In shaded conditions, effective interception of the low irradiances is essential to maximise carbon gain whereas for the leaves at the top of the canopy the efficiency of light interception is less crucial.

Foliar respiration has important consequences to stand productivity. It is generally thought that there is an upper limit of foliage biomass: as foliage area increases, availability of light in the lower foliage decreases. At some point there is not enough light available for the lower leaves to produce the amount of photosynthates required for their own
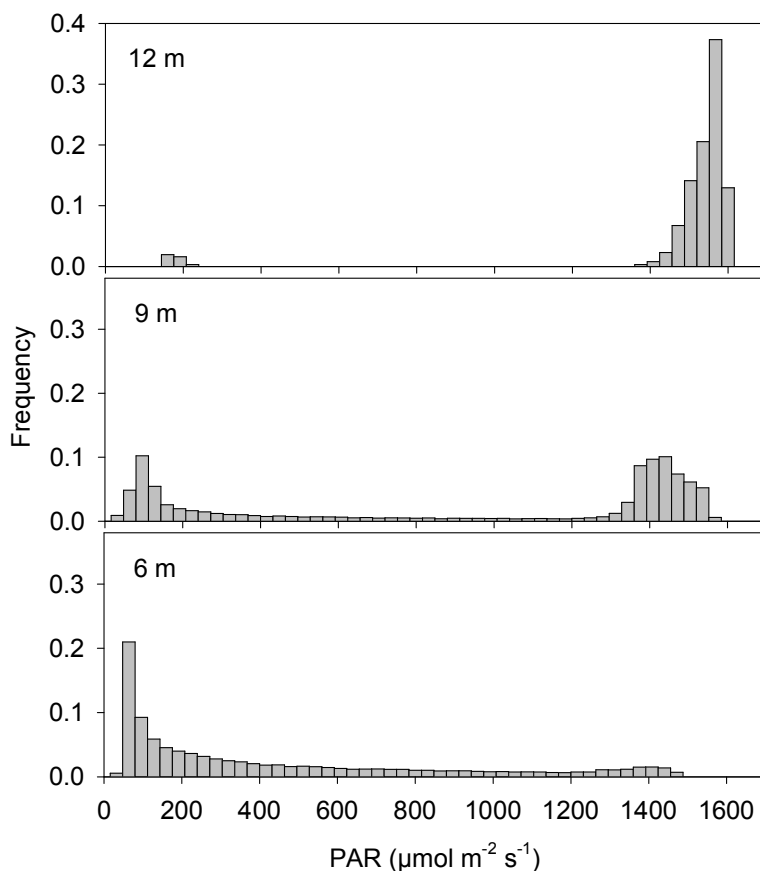
Figure 3. Spatial distributions of observed PAR at different heights in the canopy at SMEAR II. As the distance travelled by solar beams in the tree crowns increases, the distribution is shifted towards the low irradiances. The data was measured at 10-second intervals during one hour at noon on a clear summer day, with arrays of 24 or 48 PAR sensors installed on horizontal booms. The average incident PAR was 1560 µmol m^{-2} s^{-1} and the height of the canopy about 14 m.

maintenance (Oren et al. 1986). Fertility and water availability in turn determine the maximum quantity of foliage and the rate how quickly that is reached.

After canopy closure the stand foliage mass is relatively stable. In maturing stands, however, productivity is often considered to decline when the trees grow in size. There are different hypotheses why productivity in old stands would decrease (Ryan et al. 1997b): Water transport in tall trees becomes more difficult because hydraulic resistance increases with tree height. Respiration of woody structures increases with sapwood biomass. Sequestration of nutrients in biomass and detritus of old stands will reduce productivity. However, none of these hypotheses have been proven applicable in all cases (e.g. Niinemets 2002, Ryan et al. 2004). Respiration per unit biomass is much lower in woody tissues than in foliage (Mohren 1987), therefore the increase in woody biomass will not increase stand respiration dramatically.

Heterotrophic respiration in a forest soil is normally dominated by the consumption of root exudates in the rhizosphere and by the decomposition of easily decomposable fraction of the litter (Buchmann 2000, Högberg and Read 2006). Leaves especially contain plenty of simple carbohydrates that are rapidly utilised by the fungi, bacteria and larger animals that live in the soil. Although the amount of humus in the soil is large, CO_2 efflux from its decomposition is only a minor fraction of the total heterotrophic respiration (Liski et al. 2005).

Major disturbances like thinning and clearcutting introduce large amounts of dead biomass into the ground. In managed forests the decomposition of cutting debris, stumps and roots is a significant part of the CO_2 exchange after disturbances and in the early phases of the stand development and turn the stand to a source of CO_2 for many years or even decades after clearcutting (Janisch and Harmon 2002, Kowalski et al. 2004, paper I). The amount of slowly decaying woody debris remains considerable for years or decades after disturbance because it takes time for the microbes to colonise and decompose the coarse woody debris that mainly consists of cellulose and very decay-resistant lignin. The rate of the decomposition of the cutting residue is related to time since the intervention rather than to the structure of the stand. The vegetation in the stand, however, can indirectly affect the decomposition rate by modifying the conditions in the ground. Transpiration decreases soil water storage and interception of solar radiation by the vegetation decreases input of radiative energy into the ground. The stand becomes again a sink of CO_2 when the accumulation of carbon into the regenerating vegetation exceeds the release of carbon from the decaying biomass.

DETERMINING CARBON DIOXIDE FLUXES IN A FOREST STAND

The exchange of CO_2 between the forest stand and the atmosphere results from the processes binding and releasing CO_2, i.e. photosynthesis and respiration. Stand-scale fluxes of CO_2 can be determined by directly measuring the ecosystem CO_2 exchange or by upscaling, i.e. integrating, small-scale fluxes over the stand. Both these approaches require modelling, at least to some extent. Integration of small-scale fluxes requires mathematical description of the spatial and temporal variability in the environmental driving factors and in the stand structure. In stand-level measurements, models are needed to construct a continuous time series of fluxes. Simple empirical regressions that relate the observed CO_2 exchange to environmental driving factors are often sufficient for this purpose. In many cases, modelling is also needed to separate the CO_2 uptake and release processes from the measured net CO_2 exchange. A typical example is leaf CO_2 exchange that consists of photosynthetic CO_2 uptake and CO_2 efflux from respiration. Furthermore, modelling may be required to determine the actual respiration from CO_2 signal that lags the CO_2 production due to transport, e.g. in tree stems (paper V, Hölttä and Kolari 2009).

Chambers

Chamber measurements are an indirect method of determining gas exchange; the effect of the object being studied on its own environment is determined. In practise, the studied

object is enclosed inside a chamber and the rate of CO_2 exchange is calculated from the mass balance of CO_2 inside the chamber. As any source or sink creates concentration gradient around itself, the effect of the studied object on its environment can also be determined from gas concentration profiles in free air (Rannik et al. 2004) or in soil airspace (Tang et al. 2003, Pumpanen et al. 2008).

Numerous different types of chambers have been introduced for measuring CO_2 exchange of leaves, stems and ground (Figure 4). A typical chamber setup consists of chamber, sample tubing, gas analyser and a pump that draws air from the chamber. The chamber can be monitored continuously and the gas exchange calculated as the rate of throughflow multiplied by concentration difference between sample air taken from the chamber and replacement air lead into the chamber (steady state). The chamber can also be closed intermittently and the gas exchange rate calculated dynamically from the momentary change in the gas concentration inside the chamber immediately after the chamber closing.
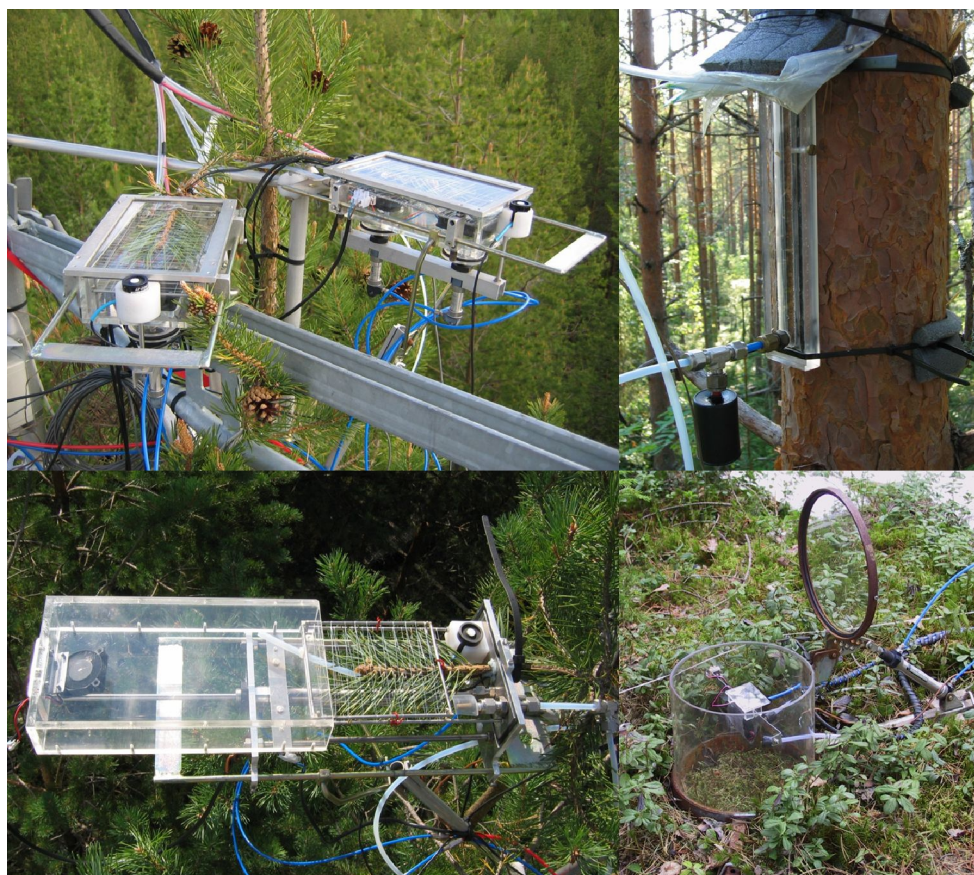

Figure 4. Different chamber designs utilised at SMEAR II for measuring gas exchange of leaves and shoots (left), tree stems (top right) and ground (bottom right).

Upscaling of chamber measurements

Information obtained from chambers can be utilised in determining gas exchange of larger entities. Numerical methods are commonly used in the integration. The stand is split into smaller elements where environmental factors can be assumed to be sufficiently constant; the instantaneous rate of CO_2 exchange is calculated for each element and finally integrated over the stand. Applying small-scale observations or modelling of CO_2 exchange to determine tree or stand level is not trivial, however: Spatial variation in the environmental driving factors increases when moving from a small element of leaf surface area towards a larger spatial scale. Ideally, the processes behind the CO_2 exchange should be studied in a spatial scale so small that the spatial variation within the object being studied is insignificant. In photosynthesis this would mean a small leaf surface element (Hari 1980). In practise working at such a small scale brings in additional uncertainty in determining the small-scale variability in the ecosystem. In field studies of photosynthesis, it is practical to use the leaf or the shoot as the basic functional unit in gas exchange measurements and modelling (Gower and Norman 1991). At a larger scale it is most convenient to separate the ecosystem into compartments that have similar within-compartment functional connections between the biological processes and the environmental driving factors. In a typical case of determining the CO_2 exchange of a forest stand, different canopy layers or tree species, photosynthesis, respiration of foliage, respiration of aboveground woody tissues, and respiration of roots are determined separately. In addition to the respiration of living plants (autotrophic respiration), CO_2 efflux from decomposition in the soil (heterotrophic respiration) can be determined either mechanistically based on the inputs of litter and root exudates into the soil (e.g. Hari et al. 2008), or empirically as a function of, for instance, soil moisture and temperature (e.g. Pumpanen et al. 2003).

Radiative transfer in the plant canopy is prerequisite for determining canopy photosynthesis from shoot-scale observations or models of photosynthesis. The most notable differences between the various integration approaches in determining canopy gas exchange are related to how the variability of light in different parts of the canopy is considered (Kolari and Hari 2008, Figure 5). As a first approximation, the irradiance distribution can be reduced to one mean value of irradiance, or irradiance at any given point is calculated from above-canopy radiation as a function of shading canopy elements above the observation level, using the Lambert-Beer law of extinction (big-leaf models, Sellers et al. 1992). The accuracy of light environment calculations can be improved if the angular distribution of incident light is considered and total irradiance separated to direct and diffuse components. Foliage area can be divided into leaves or shoots that are illuminated by both diffuse light and direct beam (sun leaves or shoots), and shade leaves or shoots that are only receiving diffuse light. The accuracy of determining the light environment can be further improved by treating the irradiance at each level as a distribution instead of a single value or a pair of shade and sunfleck irradiances.

The within-crown light distributions can be determined empirically from measurements at several locations inside the canopy. For example, Ross et al. (1998) developed empirical relationships between shading foliage area and irradiance distributions in a willow coppice. Those relationships were further modified for SMEAR II stand (Vesala et al. 2000, paper IV). Incident photosynthetically active radiation is divided into direct and diffuse components. Attenuation of the radiation components and probability of a given point at the forest floor to fall into sunfleck, penumbra or shade category were calculated as a function

of the distance travelled by the beam inside the canopy to give the momentary fractional areas of sunflecks, shade and penumbra and the corresponding irradiances.

Analytical approach for deriving the irradiance distributions (Stenberg 1996) is utilised in stand photosynthesis model SPP (paper III). The model assumes a canopy consisting of identical trees randomly distributed over stand area. Tree crowns are described as ellipsoids filled with shoots randomly distributed within the crown volume. The canopy foliage mass is distributed evenly inside the individual crowns, i.e., there is no explicitly defined structure inside the crowns (Figure 5C). The internal structure of the crown is condensed into an aggregated parameter k, which is equivalent to the Lambert-Beer light extinction coefficient. The tree crown is divided into volume elements and the light environment in each volume element is calculated. Irradiance at a given point in the canopy is calculated as a function of the distance through the neighbouring crowns intersected by the beam plus the distance from the crown surface to the point of observation. Attenuation of the direct and diffuse radiation components is calculated separately. The canopy is further divided into sun shoots illuminated by both direct beam and diffuse radiation, and shade shoots that are only receiving diffuse light.
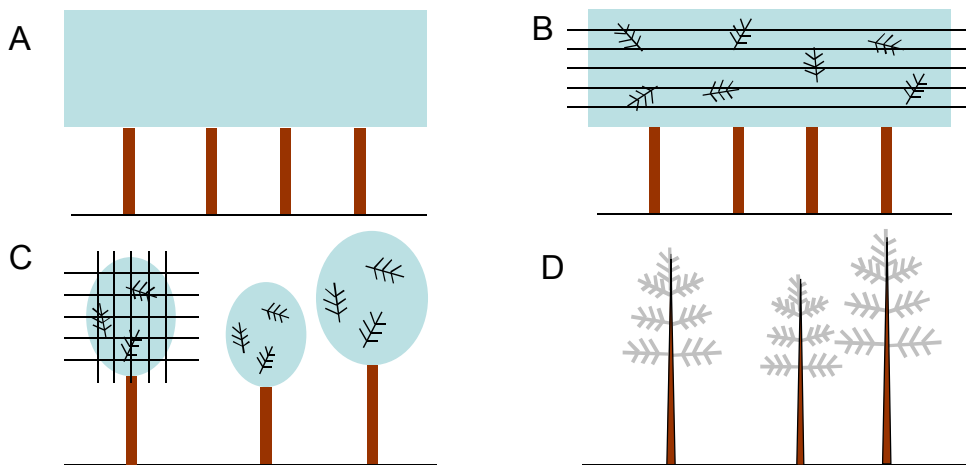
Figure 5. Different ways to describe canopy structure in calculating the distributions of the environmental driving factors in the canopy and the rate of tree or stand photosynthesis. Foliage is indicated with grey shading. (A) Big-leaf approach considers the whole forest stand as a giant leaf without internal structure. Incident light is used as the driving factor for photosynthesis, the spatial variation in light is either not considered or it is taken into account by integrating idealised vertical distribution of light within the canopy. (B) Homogeneous canopy without individual trees. Vertical gradient in light and possibly in photosynthetic parameters is considered by stratifying the canopy vertically into layers that each receive different amount of light depending on how much there is shading foliage area above the layer. (C) Individual trees with crowns consisting of homogeneous matter, vertical and horizontal gradient in light. The crowns can be divided into volume units. Light intensity in each volume unit is calculated from shading by the other volume units and shading by neighbouring trees. (D) Individual trees with explicitly defined three-dimensional branch and shoot architecture. Adopted from Kolari and Hari (2008).

Direct measurement of stand CO_2 exchange

Eddy covariance is a method to measure turbulent transport of energy and matter between the land ecosystems and the atmosphere (Figure 6). It directly gives the net gas exchange of the whole ecosystem (Net Ecosystem Exchange, NEE). The measuring system consists of an ultrasonic anemometer that measures the 3-dimensional wind speed components and an infrared gas analyser that simultaneously monitors gas concentrations in the air parcels moving through the anemometer. Measuring frequency is approximately 10 times per second. Fluxes are normally calculated as half-hourly means (Aubinet et al. 2000). The instantaneous amounts of heat or matter transported up and down are determined and the mean flux during the averaging period is the mean over all transport events. Post-processing of the fluxes involves several steps, such as corrections for system frequency response limitations and low-frequency underestimation (e.g. Rannik et al. 2004) and in some cases correction for sample air density fluctuations (Webb et al. 1980). Finally, the change in storage of CO_2 below the measurement level must be added to the observed turbulent flux to obtain the ecosystem CO_2 exchange.

The net CO_2 exchange detected by eddy covariance can be considered as a sum of two component fluxes of opposite direction. These are the combined CO_2 uptake of all vegetation layers (gross primary productivity, GPP) and CO_2 release that results from all respiratory processes (ecosystem respiration, R_e). Normally only these major component
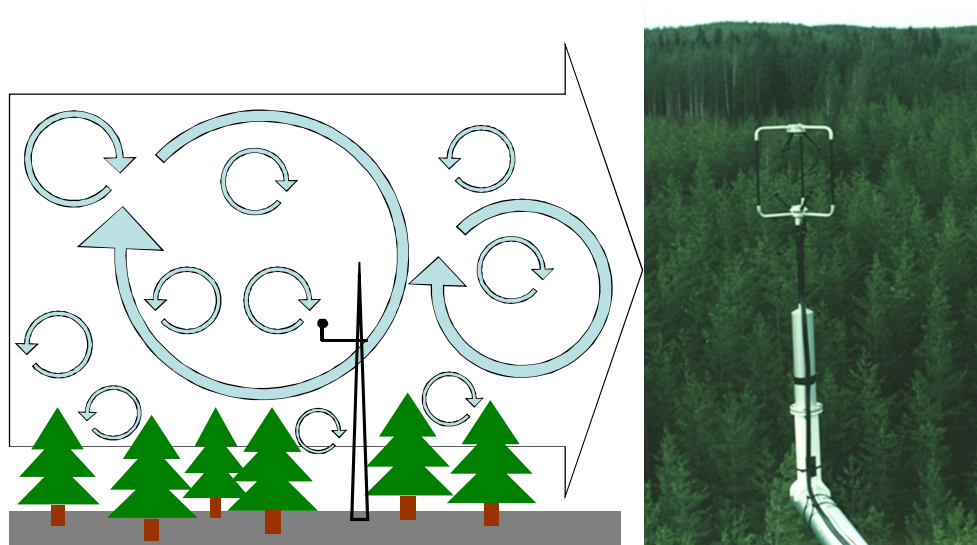
Figure 6. Schematic of turbulence and eddy covariance (left) and a 3-D ultrasonic anemometer over the forest stand at SMEAR II (right). Turbulence is created when the horizontal flow of air is redirectioned by obstacles (mechanical turbulence) or when the air near the surface warms and rises up (convective turbulence). The instrumentation represents so called closed-path setup where the sample air is drawn along sample tube from the immediate vicinity of the anemometer into a gas analyser that is located several meters from the anemometer.
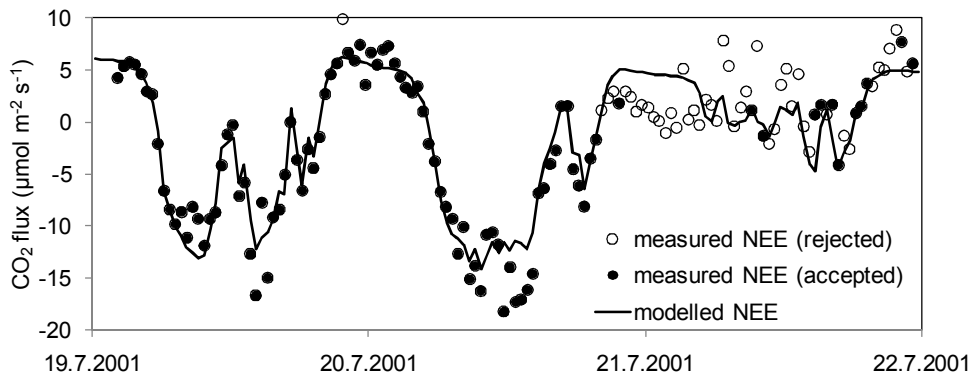
Figure 7. Ecosystem CO_2 exchange at SMEAR II measured by eddy covariance (dots) and modelled with a simple gapfilling model (solid line) over three days in July 2001. The gapfilling model was fitted to accepted turbulent flux data (indicated by closed circles). Open circles represent measurements rejected due to low turbulence; they are replaced with modelled CO_2 exchange when calculating daily and annual carbon budgets. The graph follows so called atmospheric sign convention: Negative values indicate CO_2 uptake by the forest (the atmospheric CO_2 storage decreases), positive values CO_2 efflux from the forest. The details of the gapfilling model can be found in paper V. Redrawn from Kolari et al. (2008).

fluxes are extracted from eddy-covariance data. Different subcomponents of GPP and R_e are harder to separate. The noise in half-hourly flux measurements as well as the uncertainty of determining day-time respiration limit the number of different CO_2 exchange components that can be extracted reliably and the number of model parameters that can be estimated from the flux data.

Eddy covariance fails to detect the actual ecosystem exchange under stable atmospheric stratification when there is little turbulent vertical movement of air, especially at night (Aubinet 2008). Therefore, measurements that are expected to be biased, are rejected and replaced with calculated values that are based on the accepted fluxes (Figure 7). This procedure is called gapfilling (review of methods in Falge et al. 2001). The most common gapfilling procedure is based on employing simple empirical models for ecosystem respiration and photosynthesis and using the accepted flux data to estimate the values of the model parameters. The missing or rejected fluxes are then calculated as the combination of modelled photosynthesis and respiration.

STUDY SITES AND MEASUREMENT SETUPS

This study utilised measurements of CO_2 exchange at four stands of 4, 12, 40, and 75 years of age (paper I). All sites were of medium fertility (*Vaccinium* type in Finnish site type classification, Cajander 1949) with Scots pine (*Pinus sylvestris* L.) as the dominant tree species.

The most intensively studied 40-year-old stand is surrounding the SMEAR II (Station for Measuring Forest Ecosystem-Atmosphere Relations) research station of the University of Helsinki. The station was built in 1994–1995 to provide versatile measurements of the exchange of energy and mass between the atmosphere and the forest ecosystem. The SMEAR II measuring station and the instrumentation are documented in more detail in Hari and Kulmala (2005). The instrumentation relevant to the present study is described in papers I–V.

The other studied stands were located within 5 km from SMEAR II station, paper I summarises the sites' characteristics. The amounts and the annual changes of stem, branch, needle and root biomasses for each tree species in the stands were estimated by expanding the measured height and diameter distributions through allometric equations (Marklund 1988). The sampling protocol varied somewhat from site to site due to the vastly different stand structures (paper I, Ilvesniemi et al. 2009). Soil carbon stocks at the study sites were determined from soil cores or by digging 6–8 pits at the site and taking several small soil samples from each soil layer (O, A, B, C) in each pit (paper I, Pumpanen et al 2003).

At SMEAR II station, an automated measuring system is employed for monitoring gas exchange of trees and the forest floor. The monitoring is going on continuously throughout the years, including winters, apart from short breaks due to maintenance, thunderstorms or occasional instrumentation failure. More details of the setup have been presented by Hari et al. (1999), Altimir et al. (2002) and in paper II for the shoot chambers, by Pumpanen et al. (2001) and in paper V for the soil chambers, and in paper V for the stem chambers. Soil CO_2 effluxes were also measured campaign-wise with manual chambers (paper I). At SMEAR II where the automated chambers were operated continuously, these measurements also served for determination of the spatial variability in the soil fluxes and for improving the accuracy of the absolute level of the fluxes.

The chamber data were utilised in two ways. First, measurements of the component CO_2 fluxes were upscaled directly to the stand level, and the photosynthesis and respiration models were only used as gapfilling tools. The second approach was to predict the ecosystem fluxes using generic model parameter values estimated from a large set of chamber data.

Photosynthesis of the Scots pine shoots was analysed using the model of optimal stomatal control of photosynthesis. Measurements of CO_2 exchange and transpiration from several shoots and years were used for estimating the parameter values for the photosynthesis, respiration and the annual cycle models (paper II) and further utilised in the subsequent studies (papers III, IV and V). Photosynthesis of tree foliage was integrated to the stand level with the stand photosynthesis model SPP (paper III). Canopy light extinction coefficient and the parameter values for the light attenuation model in paper IV were estimated from measurements of PAR at several locations within the tree canopies and above the forest floor (Vesala et al. 2000, Palva et al. 2001).

Photosynthesis of ground vegetation was modelled with the same principles as tree photosynthesis but using more simple models of photosynthesis (paper IV). The annual cycles of light-saturated photosynthesis in ground vegetation and photosynthetic efficiency β for Scots pine were calculated from the temperature history (papers II and IV).

The respiration components were modelled with exponential temperature response functions, parameters were estimated from night-time CO_2 fluxes. To account for the seasonal variation, the basal level of respiration, i.e. respiration at a reference temperature, was estimated in a moving time window of 5–9 days. Further details and references to the respiration modelling can be found in paper V.

The ecosystem CO_2 exchange was measured with two closed-path eddy-covariance measuring systems, the permanently installed setup at SMEAR II, and a similar setup that was moved from site to site in 2000–2002. Site-specific documentation of the EC measurements was given by Rannik et al. (2002), in paper I and by Vesala et al. (2005). Normal post-processing procedure (Rannik 1998, Rannik et al. 2004) was applied to the raw data. The half-hourly averaged data were filtered by applying thresholds of turbulence and atmospheric stability (Markkanen et al. 2001, paper I) and corrected for storage of CO_2 below the measuring height. The measured fluxes were gapfilled and separated into GPP and ecosystem respiration as documented in papers I and V.

RESULTS AND DISCUSSION

Temporal variation and driving factors of CO_2 fluxes

Relative importance of different environmental drivers to CO_2 exchange at SMEAR II stand varies with varying temporal scale. In the short term, especially in the summer, incident radiation and saturation deficit of water vapour in the air (VPD) explain most of the temporal variability in the shoot and stand GPP (papers II, III and V). CO_2 exchange is further modified by stomata that must allow CO_2 uptake while simultaneously limiting loss of water vapour. The stomatal action is frequently attributed to feedback from mesophyll CO_2 concentration (Ball et al. 1987, Leuning 1995) and response to air humidity. The actual operating principles, however, are probably more complicated (Eamus et al. 2008). The apparent VPD response may actually be response to changes in leaf water potential as a result of transpiration driven by VPD (Monteith 1995). Also transport of photosynthates in the phloem is connected to the rate of water flow in the xylem (Hölttä et al. 2006). The effect of low soil water availability on stomatal action was only observed in exceptional conditions (Duursma et al. 2008, paper V).

Outside the growing season, photosynthetic rate was more clearly related to temperature than in the summer (papers II and III). The seasonal pattern of photosynthetic efficiency in Scots pine in the southern boreal zone as well as in the northern boreal timberline consistently followed the leaf temperature history, exhibiting a saturating response to the temperature history (paper II). The deviations of the observed photosynthetic efficiency from the efficiency predicted from the temperature history could be attributed to a more rapid response of photosynthesis to low temperatures and night-time frosts. The differences in the observed relationships between photosynthetic efficiency and the temperature history were small between the southern boreal and the northern boreal trees. Also the rate of spring recovery (time constant τ in the state of acclimation S, eq. 5) was similar in the north and in the south.

The seasonal course of GPP at the stand level was predicted accurately by the delayed temperature response of photosynthetic efficiency (papers III, IV, V). This concept was also tested with a larger dataset consisting of seven coniferous stands in Europe and North America (Mäkelä et al. 2008). The annual cycle of photosynthesis was clearly temperature-driven in boreal and temperate ecosystems whereas in warmer climate the timing and magnitude of the summer drought was more important. Reichstein et al. (2007) concluded that biological activity in European forests north of approximately 52° latitude is primarily temperature-driven. In the southern Europe, photosynthesis in the summer is regularly limited by drought whereas in winter and spring the conditions are more favourable. Jung et

al. (2007) identified a positive influence of high radiation and temperature and low rainfall on summertime GPP in the northern Europe whereas in the south the relationship was negative.

In autumn above-zero temperatures often allow photosynthetic production to continue but the actual photosynthetic production is low due to low light and short daylight hours. EC-based GPP at SMEAR II in October in 1997–2007 was on average 76% of GPP in April although the monthly mean temperatures were almost equal (3.5°C in April and 4.1°C in October).

The instantaneous temperature response of photosynthesis was omitted in the present study and in earlier studies of optimal stomatal control of shoot photosynthesis (e.g. Hari and Mäkelä 2003, Mäkelä et al. 2004) as well as in the modelling study of stand photosynthesis by Mäkelä et al. (2008). Temperature response of CO_2 assimilation in Scots pine has been found to be relatively weak and the photosynthetic rate fairly stable over a wide range of temperatures (Linder and Troeng 1980, Wang et al. 1996, Aalto 1998). Omitting the instantaneous temperature responses also helped keeping the model of optimal stomatal control fairly simple. The values of the parameters can be estimated relatively easily, also from field data where radiation, temperature and VPD are intercorrelated. Temperature responses of the different subprocesses of photosynthesis are explicitly defined in the frequently used biochemical model (Farquhar and von Caemmerer 1982). Taking into account the instantaneous temperature responses will result in relatively smaller seasonal variability in the parameters describing photosynthetic capacity (Thum et al. 2007). Delpierre et al. (2009) used EC data for analysing the connection between spring photosynthesis and the environmental driving factors. They concluded that the slow acclimation to temperature dominates the springtime recovery of photosynthesis during most of the spring at SMEAR II. The instantaneous temperature had most notable influence at low temperatures.

The weak apparent temperature response may originate in the rates of subprocesses in the pathway of CO_2 into the chloroplasts: Diffusion of CO_2 in air and cytoplasm is accelerated in increasing temperature whereas dissolving of CO_2 in the water film on the mesophyll cell walls becomes slower (e.g. Ethier and Livingston 2004). When derived from field measurements, the temperature response is also, to some extent, embedded in the photosynthetic light response and in the stomatal response to VPD because short-term variations in light, temperature and water vapour concentration deficit in the air are intercorrelated. In the photosynthesis model, the delayed temperature response naturally also compensates for the lacking instantaneous response in a seasonal or annual time scale.

The mechanisms behind the delayed temperature response cannot be concluded from CO_2 exchange data only. Studies of chlorophyll fluorescence, however, suggest that low-temperature downregulation of photosynthetic capacity is most obvious in spring when there is plenty of sunlight (Porcar-Castell et al. 2005). On the dim days of late autumn and midwinter photosynthesis shows a more rapid response to rising air temperature than in spring (Hari and Bäck 2008).

The interannual variability of EC-based and modelled stand GPP was fairly small, approximately 100 g C m^{-2} a^{-1}, or 10% of the annual GPP. Despite the good agreement in within-year fluxes, the GPP predicted with SPP could not fully explain the observed year-to-year variation in GPP determined from eddy covariance; the predicted GPP in 2004 was clearly lower than the EC-based GPP (paper V). The moist conditions in the summer of 2004 may have favoured photosynthesis of trees and ground vegetation despite the slightly lower than average summertime temperature (paper V). The contribution of mosses to

stand GPP is so small, in the order of 5% (paper IV), that the decline of stand photosynthetic rate due to mosses drying out cannot be distinguished from the EC fluxes.

The respiratory fluxes generally followed seasonal patterns similar to their obvious driving temperatures, i.e. air temperature for aboveground respiration components, and soil temperature for soil CO_2 efflux (paper V). There were consistent deviations, however: Compared to predictions with the average apparent temperature responses respiration of shoots and stems were higher in spring and early summer and smaller in late summer and autumn. The higher spring and early growing season respiration compared to autumn may also be explained by growth respiration although the peak occurred before the peak in growth. This discrepancy in the timing could originate in better availability of sugars as substrate for respiration due to higher photosynthetic production and release of carbohydrates from the internal storage pools.

The respiratory fluxes responded in a similar way during the periods of anomalous weather. Soil CO_2 efflux showed the greatest drop during the drought. The aboveground respiration components (foliage and stem) decreased relatively less during the drought and also increased relatively more than soil CO_2 efflux when temperatures increased in the extremely warm early winter of 2006–2007 (paper V). The lack of increase in soil CO_2 efflux in late autumn 2006 suggests that respiration in the soil is more substrate-limited than the aboveground respiration components. The difference between the instantaneous temperature sensitivity and the apparent seasonal temperature response reflects the varying importance of different driving factors and limitations at different time scales. Long-term sensitivity larger than the instantaneous response may indicate substrate limitation; availability of sugars for respiration is better during the warm season when also photosynthetic production is at its highest (e.g. Gu et al. 2004).

Partitioning of net CO_2 exchange

The partitioning of net carbon exchange into photosynthesis, biomass increment and respiratory fluxes at SMEAR II is summarised in Figure 8. Figure 9 shows a summary of annual component CO_2 fluxes from eddy covariance and ground-based estimates of net ecosystem productivity (NEP) at the study sites. The variation of net CO_2 exchange among the study sites can be largely attributed to their different annual photosynthetic production and to the amount of decomposing cutting residue (paper I). The biggest changes in the carbon balance and in the partitioning of CO_2 exchange occur at the beginning of the stand development. Stand GPP at the 12, 40 and 75-year-old sites was similar although the contribution of trees increased and the GPP of the ground vegetation decreased with stand age (Figure 9). At the 12-year-old sapling site the foliage area of trees was small and the ground vegetation still received plenty of light; the model of light interception (Stenberg 1996) used in the stand model SPP indicates that light intercepted by trees was only in the order of 20% of incident radiation whereas in the 40- and 75-year-old stands with nearly closed tree canopy the fraction of was 70–75%. Thus, the ground vegetation at the 12-year-old site had roughly the same photosynthetic production as the trees whereas in the older stands the ground vegetation GPP was <15% of stand GPP.

The difference in annual GPP between the 40-year-old and 75-year-old stands can be explained by the slightly smaller foliage biomass of the older stand and by the crown architecture; Assuming constant stand leaf area index (LAI), light interception by
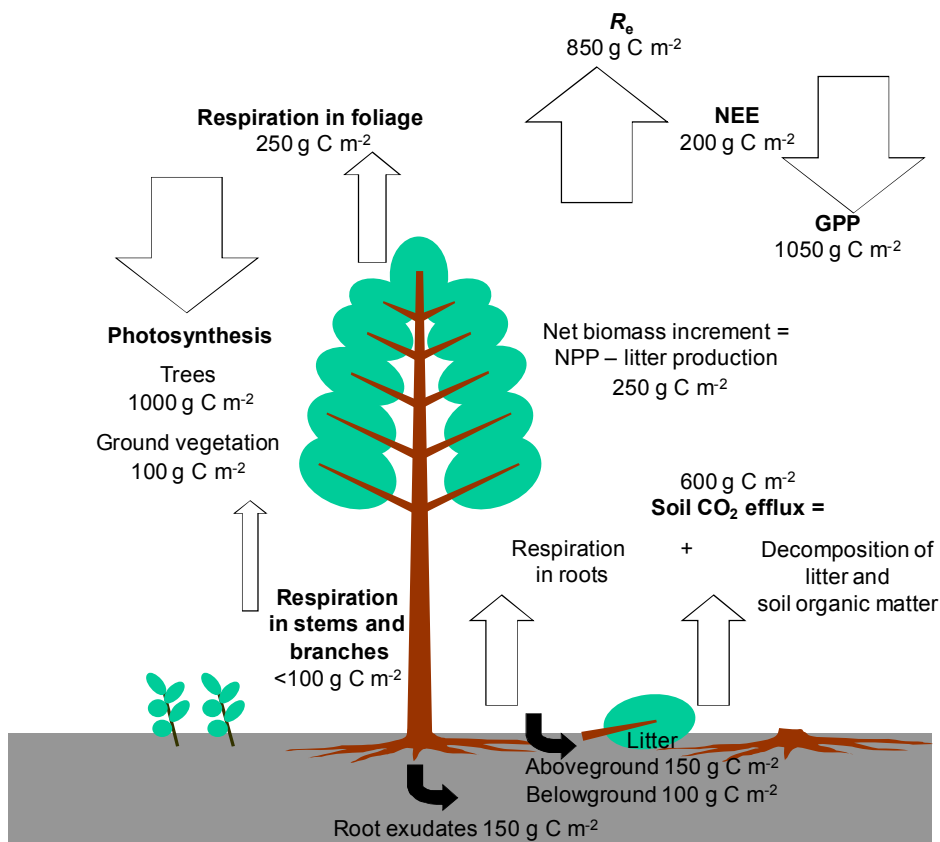
Figure 8. Typical magnitudes of annual carbon flows at SMEAR II. The CO_2 fluxes are based on paper V, biomass increment and litter production on Ilvesniemi et al. (2009), root exudates on Pumpanen et al. (2008). Items labelled in **bold** face indicate the fluxes that this study particularly addressed. Respiration of ground vegetation is embedded in the soil CO_2 efflux. Accumulation of biomass into the ground vegetation is unknown but probably very small.

several small crowns is more efficient than by few big crowns (Duursma and Mäkelä 2007), which may explain the difference in stand GPP between the 40 and 75 yr stands.

The normal seasonal variation in the foliage area contributed little to the annual pattern of stand photosynthesis at SMEAR II. Seasonal variation in LAI in Scots pine is roughly 25% of the seasonal maximum which corresponds to variation of less than 10% in photosynthesis in a typical closed-canopy stand. Furthermore, photosynthesis by ground vegetation can compensate for the change in tree photosynthesis. The partial thinning at SMEAR II in 2002 did not change total stand GPP considerably (Vesala et al. 2005). The seasonal maximum of all-sided LAI decreased from approximately 8 to 6.5 (19%) which decreased the radiation intercepted by the tree canopy by mere 8% and GPP by 70 g C m^{-2} a^{-1}, or 6%. On the other hand, light reaching the ground vegetation increased approximately 30% which corresponds to similar relative increase (approx. 30 g C m^{-2} a^{-1}) in GPP. The change in stand GPP is of the same order as the annual random uncertainty in EC (40 g C m^{-2} a^{-1}, paper V), thus it could not be detected reliably. The effect of
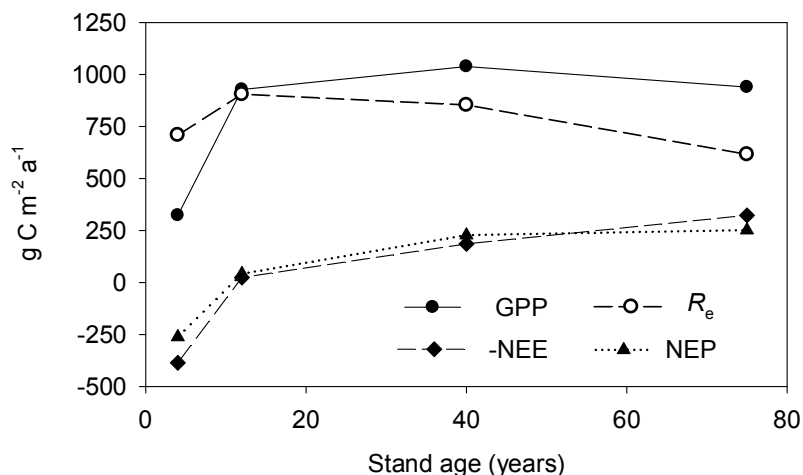
Figure 9. Annual net ecosystem exchange (NEE, negative sign for convenience), photosynthesis (GPP) and respiration (R_e) from eddy covariance in four different aged Scots pine stands (paper I). Net ecosystem productivity (NEP) is based on biomass inventories and modelled decomposition of cutting residue, positive values indicate carbon uptake by the stand, negative loss of carbon from the stand to the atmosphere.

thinning was further obscured by the weather-driven variability in annual NEE and component fluxes.

The measured ecosystem respiration at the study sites of different ages (paper I) can be partitioned into autotrophic components by scaling the respiration components by biomass at each study site compared to biomasses at SMEAR II stand in 2000–2001 (Figure 10). Heterotrophic respiration can be approximated from the estimated decomposition of cutting debris (paper I) and from the litter production. Once the majority of the cutting residue has decayed, also heterotrophic respiration is constrained by productivity (Bond-Lamberty et al. 2004) unless substantial decrease in the old soil C pool takes place. Therefore, it can be concluded that in the older stands CO_2 from decomposition is of similar magnitude as the annual input of dead biomass. The annual aboveground litter input in the SMEAR II stand was 150–200 g C m^{-2} and fine root turnover about 90 g C m^{-2} (Ilvesniemi et al. 2009). At the 75-year-old site these values were similar and the proportion of heterotrophic respiration from total respiration was roughly 35–40% (half of soil CO_2 efflux). At the 12-year-old sapling site the litter production was smaller but the decomposition of residual roots and stumps more than compensated that which resulted in the contribution of heterotrophic respiration of about 40%. At the clearcut site the heterotrophic respiration dominated with a proportion of >60%. It is reasonable to assume that autotrophic respiration, i.e. consumption of photosynthate, cannot exceed photosynthetic production in the long term. Thus the annual autotrophic respiration at the clearcut site (paper I) was no more than approx. 300 g C m^{-2}, less than half of the ecosystem respiration (approx. 700 g C m^{-2}).

There are big uncertainties in determining the rates of root growth and growth respiration, release of root exudates and decomposition of organic matter simply because belowground processes are harder to observe and quantify than, for example,

photosynthetic production. It is also important to distinguish between mechanisms that release carbon to the atmosphere and those that transport it away from the stand or transfer it to humus (Yanai et al 2003). A small part of the organic carbon is dissolved in the soil water and flushed away from the site by infiltration or runoff. At SMEAR II the amount of carbon lost by runoff is, however, negligible (Ilvesniemi et al. 2009). The processes of decomposition also produce decay-resistant humic substances that have residence time of hundreds or thousands of years in the soil (Liski et al. 2005). Decomposition of this "old" soil organic matter is poorly known. There was no trend in the soil C stock in the studied chronosequence and changes in soil C stock over rotation time are in general very small (Liski and Westman 1995) which suggests that the old C does not have a significant contribution to the ecosystem respiration.

The interannual variability of GPP and R_e from eddy covariance was in the order of 10% even though there were very dry (2002 and 2006) and rainy summers (2004, for instance) in the studied period. The annual NEE, however, varied relatively more, approximately ±25%. The interannual variability of NEE can be largely explained by tree growth (Ilvesniemi et al. 2009). In regions where drought periods are more severe, the interannual variability may be greater (Schaefer et al. 2002).

The interannual variation of EC-based GPP and R_e at SMEAR II largely compensated each other so that GPP, R_e and NEE were all correlated with each other (paper V). This observation supports the hypothesis that respiration in the long term is driven by supply and demand and largely indirectly by the environmental drivers (Janssens et al. 2001). In CO_2 enrichment experiments, root respiration has been observed to increase as response to increased supply of photosynthates (Zak et al. 2000). The reduction in the demand for photosynthates taking place at low temperatures is suggested to inhibit photosynthetic production (Savitch et al. 2002, Hjelm and Ögren 2003). Photosynthates can be stored as starch, but eventually their production must be reduced to match the consumption. Girdling experiments have shown that removing the below-ground sink decreases photosynthetic production (Högberg et al. 2001). Ensminger et al. (2008) found that recovery of photosynthetic capacity was slowed down by cold and frozen soil. Furthermore, Bergh and Linder (1999) found that heating the soil lead to increased light-saturated rate of photosynthesis in spring. In typical spring conditions, however, the role of belowground sink limitation, i.e. cold soil, in the annual cycle of photosynthesis might be less obvious. As long as the ground is not frozen, trees can possibly release photosynthates as root exudates to discard the excess production (Trumbore 2006).

Carbon balance over stand life cycle

The SMEAR II stand was a sink of carbon in all years (1997–2007) when full year of EC data was available (Markkanen et al. 2001, Suni et al. 2003b, paper V). The annual NEE varied between 136 and 241 g C m^{-2} a^{-1} when the gapfilling was done following the procedure in paper V. This corresponds to woody biomass increment of 7–12 m^3 ha^{-1} assuming biomass C content of 50% and wood density of 400 kg m^{-3}. The site clearfelled four years before the flux measurements was a source of approximately 400 g C m^{-2} a^{-1} (paper I), the C source was comparable to other recently clearfelled sites (Amiro 2001, Kowalski et al. 2004). Flux measurements at the 12-year-old stand indicate that a developing Scots pine stand turns from source of CO_2 to a carbon sink at the age of 10–15
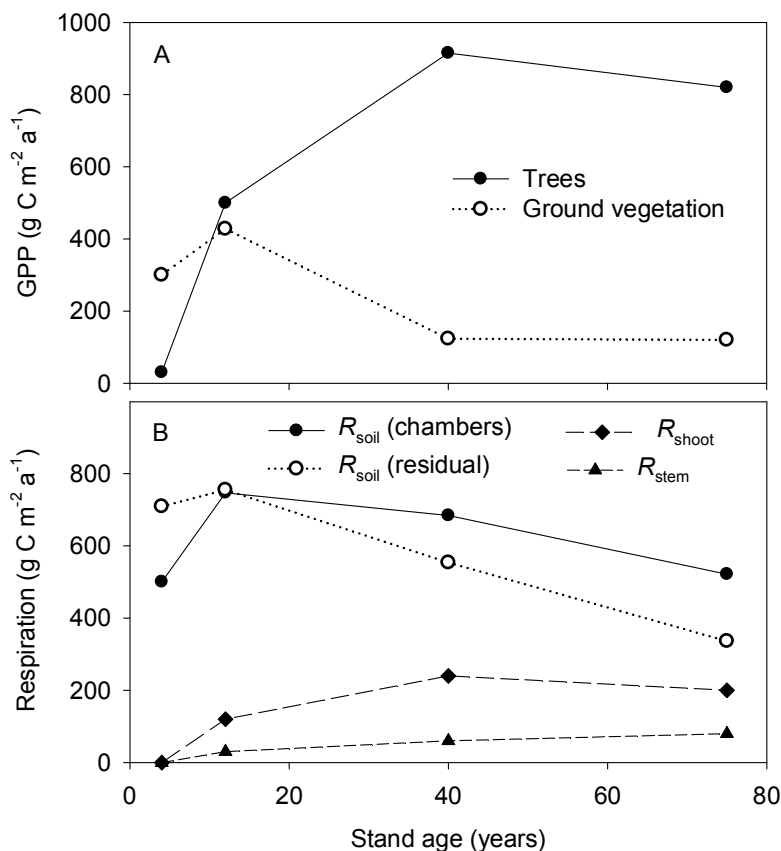
Figure 10. Annual photosynthetic production of trees and ground vegetation (A) and respiration components (B) at the study sites as a function of stand age. The estimates of photosynthesis are based on simulations with stand photosynthesis model SPP. Two independent estimates of soil CO_2 efflux (R_{soil}) are given: direct measurement by manual chambers in 2002, and "residual" R_{soil} estimated as the difference between the EC-based R_e and modelled aboveground respiration. For the clearcut site, the residual R_{soil} is based on EC fluxes measured in 2000 whereas the chamber-based R_{soil} was measured in 2002.

quickly the carbon-binding trees are regenerated and on the amount of debris left at the site on the clearcutting. Karjalainen (1996) obtained similar results based on modelling. The release of large amounts of CO_2 during the first years after stand-replacing disturbance mean that the carbon sink integrated over the stand life cycle is only about half of the C sink based on flux measurements in middle-aged forest stands (Magnani et al. 2007).

Carbon sink strength at the 75-year-old site did not show any signs of age-related decline. It is probable that a frequently thinned Scots pine stand can sequester great amounts of carbon far beyond the usual economic rotation length of 80–100 years due to the very small production of coarse woody debris. Decomposition of cutting residue is also a slow process. Part of the SMEAR II stand was thinned in early 2002 but the thinning did not show up at all in the flux measurements (Vesala et al. 2005). Once the majority of the

woody debris from the clearcutting has decayed, the net carbon uptake of a managed forest stand is close to the net biomass increment in trees, i.e. NPP minus litterfall (e.g. Schelhaas et al. 2004, Ilvesniemi et al. 2009).

Respiration is often expected to continuously increase as woody debris accumulates in aging forests, and to eventually balance photosynthesis. However, CO_2 efflux from woody debris decomposition may be insignificant even in old-growth forests (Tang et al. 2008). Provided that the canopy remains fairly closed, the carbon sink remain strong for centuries until the trees reach the end of their life span (Luyssaert et al. 2007b, Tang et al. 2008). For long-living species such as pines this may take hundreds of years unless catastrophic stand-replacing disturbance like fire occurs. New trees will also emerge in the gaps left by fallen old trees, thus there will be photosynthetic production and accumulation of biomass going on continuously. Net primary production is generally thought to decline in aging forests (Ryan et al. 1997b) but despite the possibly weaker annual carbon sequestration, old forests are important as carbon stocks. The aboveground C stock of the 75-year-old study site was about 100 t C ha^{-1} (paper I) whereas the possible upper limit could be several times higher (Luyssaert et al. 2007b).

Uncertainties in the CO_2 fluxes

Annual GPP, R_e and NEE from eddy covariance generally agreed well, within the range of uncertainty, with the upscaled fluxes. Year-to-year variation in the annual EC-based GPP, R_e and NEE in the SMEAR II stand was small, the ranges of variation were just over 100 g C m^{-2} a^{-1}. It is important to understand how accurately the net CO_2 exchange and the component CO_2 fluxes can be quantified as well as how small changes in the annual carbon balance can be detected.

The random errors in eddy covariance due to the stochastic nature of turbulence are of minor importance and mostly cancel out in the long term, the precision of the annual C budgets (NEE, GPP, and R_e) being 30–40 g C m^{-2} (paper V). According to Ilvesniemi et al. (2009), year-to-year variation was similar in biomass increment and in NEE which strengthens the confidence that the observed year-to-year variation in turbulent fluxes is real.

The systematic errors are more severe. Eddy covariance underestimates the actual ecosystem exchange under stable atmospheric stratification when there is little turbulent vertical movement of air (Aubinet et al. 2000). The turbulent fluxes are corrected for storage but CO_2 transported by advection and large eddies remains missing in the storage-corrected fluxes. Comparison of night-time turbulent fluxes with the flux estimates based on automated chambers suggest that the advective transport of CO_2 is of minor importance at SMEAR II despite the far from ideal topography of the site (Mammarella et al. 2007). On the other hand, night-time EC fluxes at the study sites were only marginally larger than soil CO_2 effluxes measured by manual chambers (paper I) which may indicate underestimation of fluxes by EC. Determination of soil fluxes naturally also suffers from systematic measuring errors (Pumpanen et al. 2001, 2004), thus it is not possible to conclude whether EC underestimates or chambers overestimate respiration.

The source area of the flux detected by eddy covariance, so called footprint, varies with wind direction, stability and turbulence. This is important if the sources and the sinks of CO_2 are not evenly distributed in the stand. Footprint was especially problematic at the small clearcut site where approximately one third of the flux data had to be excluded

because the footprint extended into the adjacent forest (paper I). At SMEAR II the source area for the tree canopy in unstable conditions may be less than 100 m whereas in near-neutral conditions the source area at the ground level extends to 200–300 m (Rannik et al. 2000). EC-based net carbon uptake was systematically lower than biomass increment within 200 m radius (Ilvesniemi et al. 2009). Within a smaller distance from the eddy tower the annual NEE and biomass increment matched better. The inventory-based methods naturally involve uncertainty of their own, the problems being largely related to determining the root biomass (Schelhaas et al. 2004) and changes in soil carbon stock (Conen et al. 2003). Using eddy covariance can circumvent the problem of repeated measurements of soil carbon stocks at recently disturbed sites where CO_2 efflux from decomposition dominates the CO_2 exchange.

One of the main shortcomings of EC, i.e. systematic errors related to turbulence, can be largely avoided using upscaled chamber measurements. Therefore, the upscaled fluxes can be utilised in analysing the systematic errors in eddy covariance (Mammarella et al. 2007, van Gorsel et al. 2007). In general, however, the systematic uncertainty in the upscaled fluxes was at least as large as in EC-based fluxes because uncertainty accumulates in the integration procedure (paper V). Calculating stand photosynthesis requires several simplifying assumptions, and the integration method is always a compromise determined by the accuracy of the information on the canopy structure, the variation of photosynthetic properties and the environmental driving factors within the canopy. In the stand photosynthesis calculations the shoots were assumed to be of the same geometry throughout the canopy, any within-tree variation of shoot morphology was omitted. Photosynthetic parameters of the top shoots were also applied to the whole crown, acclimation of shade shoots to lower light was ignored which resulted in error of about 5% in annual tree photosynthesis (Kolari and Hari, 2008) while the overall uncertainty of the integration was 10–20% (paper V).

The chamber itself affects the fluxes in two ways. First, the chamber unavoidably modifies the microclimate of the object being measured so that it is slightly different from the ambient conditions. Secondly, chemical and physical reactions on the chamber walls and sample tubing can affect observed fluxes of reactive gases as O_3 (e.g. Altimir et al. 2002). For inert gases, such as CO_2, the surface reactions are negligible (Hari et al. 1999) but H_2O fluxes that are utilised in estimating the parameter values of the stomatal model (paper II) are affected by adsorption of water molecules onto the chamber walls (Kolari et al. 2004).

One pine shoot cannot be monitored for more than approximately two years after which it must be replaced by a new one. This discontinuity can be overcome by simultaneously monitoring several shoots with overlapping measuring periods. In spite of that, long-term cumulative CO_2 fluxes taken directly from chambers still involve sampling uncertainty. A standardised non-disturbing direct flux measurement, such as EC, or prediction with more general model parameters, as in paper III, can capture year-to-year variation in fluxes more accurately than upscaling directly from chamber measurements. The particular strength of the chamber measurements is the ability to capture the spatial and short-term temporal (e.g. diurnal) variability in CO_2 fluxes more accurately than eddy covariance can do. The good temporal agreement between the EC-based fluxes and the integrated chamber fluxes over the seasons as well as during the drought (paper V) indicates that a small number of chambers can capture the dynamics of the different components of the whole forest ecosystem CO_2 exchange very well.

Concluding remarks

This study aimed to quantify and understand the dynamics of carbon balance and its partitioning into component CO_2 fluxes at different phases of stand rotation time in Southern Finland. The scope was limited to selected boreal Scots pine stands but the results can be largely applied to a vast area of boreal coniferous forests.

Carbon balance of a forest stand depends on the relationship between production and decomposition, which in turn greatly depends on the time from last disturbance. While disturbances decrease canopy closure and photosynthesis, they increase CO_2 efflux from decomposition. After major disturbance the rate of decomposition can exceed photosynthetic production for more than a decade. CO_2 efflux from the soil dominates the ecosystem respiratory fluxes in all phases of stand development. The origin of CO_2 from the soil, however, changes during the stand development: In young open stands a large part of soil CO_2 efflux is originated in decomposition of cutting debris.

The connections between stand age, carbon uptake and productivity result from changes in stand structure. At sites of similar fertility and same tree species, photosynthesis is largely determined by foliage biomass that affects the light environment in the canopy. Autotrophic respiration increases somewhat with the accumulation of biomass. Rate of wood respiration is so low, however, that the total aboveground respiration is dominated by foliage and does not increase significantly after canopy closure.

To my knowledge, paper IV was the first published study to explicitly assess the photosynthesis of ground vegetation by integrating small-scale observations over space and time. Photosynthesis of ground vegetation depends on the shading overstory. Under closed pine canopy, ground vegetation only accounts for a relatively small fraction of stand GPP whereas under open canopy the proportion and also the absolute GPP can be much higher.

Instantaneous and delayed responses can predict well the observed within-year variation in photosynthetic production: In the short term photosynthesis follows primarily light whereas the seasonal variation is more strongly connected to temperature through instantaneous and delayed responses. The temperature relationship of the annual cycle of photosynthesis is surprisingly similar in the southern boreal zone and in the northern timberline. Also the respiratory fluxes showed instantaneous and seasonal temperature relationships. The long-term temperature responses are apparent, however; during drought and in winter CO_2 effluxes were lower than predicted from temperature alone. Furthermore, the interannual variation in respiratory C budgets could not be explained by temperature. The annual carbon budgets and the fluxes during anomalous periods (e.g. drought) support the hypothesis that respiration in the long term is driven by photosynthesis rather than by environmental factors. Due to the strong link between photosynthesis and respiration, future projections based on apparent temperature responses of respiration and photosynthesis obtained from field measurements can be misleading (Saxe et al. 2001). In the present climate, growth of boreal forests is often nutrient limited and enhancement of nitrogen cycling is the key factor in the future forest growth (Högberg 2007, Magnani et al. 2007). Global warming and the increase of atmospheric CO_2 are likely to increase photosynthetic production and C fixation by the forests (Hyvönen et al. 2007, 2008). If the partitioning of photosynthesis to respiration and biomass production (Waring et al. 1998) remains in the future, NPP will also increase. Understanding the controls and partitioning of autotrophic and heterotrophic respiration still requires further study. More attention should be paid to mechanistic analysis of the connections between photosynthesis, respiration, accumulation of biomass and decomposition.

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