CANOPY PROCESSES, FLUXES AND MICROCLIMATE IN A PINE FOREST

SAMULI LAUNIAINEN

Division of Atmospheric Sciences
Department of Physics
Faculty of Science
University of Helsinki
Helsinki, Finland

Academic dissertation

To be presented, with the permission of the Faculty of Science of the University of Helsinki, for public criticism in auditorium E204, Gustaf Hällströmin katu 2a, January 7th, 2011, at 12 o’clock noon.

Helsinki 2011
Abstract

Interaction between forests and the atmosphere occurs by radiative and turbulent transport. The fluxes of energy and mass between surface and the atmosphere directly influence the properties of the lower atmosphere – and in longer time scales the global climate. Boreal forest ecosystems are central in the global climate system, and its responses to human activities, because they are significant sources and sinks of greenhouse gases and of aerosol particles. The aim of the present work was to improve our understanding on the existing interplay between biologically active canopy, microenvironment and turbulent flow and quantify. In specific, the aim was to quantify the contribution of different canopy layers to whole forest fluxes. For this purpose, long-term micrometeorological and ecological measurements made in a Scots pine (Pinus sylvestris) forest at SMEAR II –research station in Southern Finland were used.

The properties of turbulent flow are strongly modified by the interaction between the canopy elements: momentum is efficiently absorbed in the upper layers of the canopy, mean wind speed and turbulence intensities decrease rapidly towards the forest floor and power spectra is modulated by ‘spectral short-cut’. In the relative open forest, diabatic stability above the canopy explained much of the changes in velocity statistics within the canopy except in strongly stable stratification. Large eddies, ranging from tens to hundred meters in size, were responsible for the major fraction of turbulent transport between a forest and the atmosphere. Because of this, the eddy-covariance (EC) method proved to be successful for measuring energy and mass exchange inside a forest canopy with exception of strongly stable conditions. Vertical variations of within canopy microclimate, light attenuation in particular, affect strongly the assimilation and transpiration rates. According to model simulations, assimilation rate decreases with height more rapidly than stomatal conductance (g_s) and transpiration and, consequently, the vertical source-sink distributions for carbon dioxide (CO₂) and water vapor (H₂O) diverge. Upscaling from a shoot scale to canopy scale was found to be sensitive to chosen stomatal control description. The upscaled canopy level CO₂ fluxes can vary as much as 15 % and H₂O fluxes 30 % even if the g_s models are calibrated against same leaf-level dataset.

A pine forest has distinct overstory and understory layers, which both contribute significantly to canopy scale fluxes. The forest floor vegetation and soil accounted between 18 and 25 % of evapotranspiration and between 10 and 20 % of sensible heat exchange. Forest floor was also an important deposition surface for aerosol particles; between 10 and 35 % of dry deposition of particles within size range 10 – 30 nm occurred there. Because of the northern latitudes, seasonal cycle of climatic factors strongly influence the surface fluxes. Besides the seasonal constraints, partitioning of available energy to sensible and latent heat depends, through stomatal control, on the physiological state of the vegetation. In spring, available energy is consumed mainly as sensible heat and latent heat flux peaked about two months later, in July – August. On the other hand, annual evapotranspiration remains rather stable over range of environmental conditions and thus any increase of accumulated radiation affects primarily the sensible heat exchange. Finally, autumn temperature had strong effect on ecosystem respiration but its influence on photosynthetic CO₂ uptake was restricted by low radiation levels. Therefore, the projected autumn warming in the coming decades will presumably reduce the positive effects of earlier spring recovery in terms of carbon uptake potential of boreal forests.

Keywords: Forest-atmosphere interactions, canopy turbulence, photosynthesis, respiration transpiration, energy balance, Scots pine
Acknowledgements

There are numerous people who have contributed to this work during the years. I want to thank Prof. Juhani Keinonen and Department of Physics for providing the working facilities and Academy of Finland Centre of Excellence Program for financial support through the Finnish Graduate School. I am grateful for Prof. Markku Kulmala for the innovative and multidisciplinary environment which, at its best, really stimulates creative scientific thinking. I thank the pre-examiners Almut Arneth and Alessandro Cescatti for their throughout reviews.

I want to express my gratitude to my supervisor Prof. Timo Vesala whose door has always been open for discussion, science related or whichever. I hope I have absorbed a fraction of your excellent social skills and flexible attitude. I think we both have benefited from the perfectly open and honest working relationship we share. I also want to thank Prof. Pepe Hari for optimal discussions related to trees, their functioning and scientific practices in general.

I have been privileged to work intensively with Prof. Gaby Katul from Duke University since winter 2007. Gaby, you learned me how the science should be thought and how the variety of problems should be tackled. You showed what it really would take to be a Scientist: enthusiasm, creativeness, suite of problem-solving skills and wide perspective – beyond numerous working hours. Thanks for your support.

Today, research equals collaboration. Therefore, I want to thank all my co-authors and colleagues in the Universities of Helsinki, Lund and Stockholm. Especially, I owe a lot to Pasi Kolari who has shared his knowledge on forest ecology and photosynthesis modeling with me. It is fun to work with a person like you; always willing to help and always fulfilling the promises, in time. I also want to thank Liisa Kulmala and Jukka Pumpanen for discussions related to understory and boreal soils – the lower boundary of this study. Thanks also to all my colleagues at Department of Physics, Sami Haapanala, Petri Keronen, Sanna Sevanto, Eki Siivola, Ivan Mammarella, Mari Pihlatie and Janne Rinne in particular. Not to forget Üllar Rannik and his cryptic Matlab –codes I inherited. Tanja Suni, Lauri Laakso and Anca & Jukka Hienola are acknowledged on their excellent peer-support at several occasions.

This work is largely based on measurements conducted at Hyytiälä SMEAR II –station. Thank you, Veijo Hiltunen, Heikki Laakso, Janne Levula and Toivo Pohja, for all the help and assistance. Working with you on the field has been, by far, the most enjoyable part of my studies. I am also indebted to all the students I have worked with in different courses – teaching has been the best way of learning, although often undervalued in today’s academic world.

Most importantly, I want to thank all my friends and family for your support and love during the years. Tiia, thanks for being there both as a colleague and wife, the latter being my greatest achievement. With you I have experienced quite a lot, felt strong emotions in all shades of color and finally learned to master, and at times even lower, my self-criticism.

Finally, I made this thesis because I wanted to run. A few years back, my desire was to find my limits as orienteer and thought that the academic environment would be the best to combine intensive training and competing with interesting studies. So naïve I was…
# Table of Contents

Abstract ................................................................................................................................ 3  
Acknowledgements ............................................................................................................... 4  
List of publications................................................................................................................ 6  
  Authors contribution .......................................................................................................... 6  
1 Introduction........................................................................................................................ 8  
2 Aims .................................................................................................................................. 9  
3 Background........................................................................................................................ 10  
  3.1 Atmospheric boundary layer and surface energy balance ........................................... 10  
  3.2 Carbon and water in a forest ...................................................................................... 12  
    3.2.1 Photosynthesis..................................................................................................... 12  
    3.2.2 Respiration .......................................................................................................... 14  
    3.2.3 Stomatal conductance, transpiration and evaporation ........................................... 15  
4 Turbulent flow within a forest canopy .............................................................................. 18  
  4.1 Turbulent flows and Reynold’s decomposition........................................................... 18  
  4.2 Canopy turbulence ..................................................................................................... 20  
  4.3 Turbulent kinetic energy and spectra.......................................................................... 22  
5 Measuring matter and energy flows between ecosystem and the atmosphere ................. 24  
  5.1 Mass balance in turbulent roughness sub-layer flows ................................................. 24  
  5.2 Eddy-covariance ........................................................................................................ 26  
  5.3 Chambers................................................................................................................... 29  
  5.4 SMEAR II - site ......................................................................................................... 29  
6 Overview of the results..................................................................................................... 30  
  6.1 Aerosol dry deposition ............................................................................................... 30  
  6.2 Variations in microenvironment, photosynthesis and transpiration in the canopy ...... 32  
  6.3 Upscaling to canopy level .......................................................................................... 35  
  6.4 Forest floor contribution on energy and carbon fluxes............................................. 35  
  6.5 Seasonal and inter-annual variability ......................................................................... 37  
7 Overview of the papers ..................................................................................................... 41  
8 Critical opinion and future use of data ........................................................................... 43  
9 Conclusions...................................................................................................................... 46  
References .......................................................................................................................... 48
List of publications

This thesis consists of an introductory review followed by seven research articles. The papers are reproduced with the permission of the journals concerned.


Authors contribution

I am fully responsible for the summary part of this thesis and for Paper VI. In Paper I, I participated on planning and building the measurements and did all data-analysis and most of writing; In Paper II, I am responsible for all data-analysis and writing the article. Of the research papers included in this thesis, my contribution was least in Paper III, in which I am responsible for the eddy-covariance measurements and part of writing. In Paper IV, I partly
analyzed the data and wrote part of the article; In **Paper V**, I am responsible for all analysis, partly building the model and for major part of writing of the article. In **Paper VII**, my contribution spans from planning the study to analyzing the measurements and significant part of writing. **Paper III** will be included also in the doctoral thesis of Liisa Kulmala.
1 Introduction

Globally, forests span over ~42 million km\(^2\) (~30 % of land surface), contribute ~50% of the terrestrial net primary productivity and store ~45 % of terrestrial carbon (Bonan, 2008). Boreal coniferous forests cover ~7 % of the earth land surface making them the most widely distributed vegetation type in the world (FAO, 2000). Growing in the circumpolar region between 50 and 70 °N, these ecosystems have, because they lower the regional winter albedo, greater influence on mean global temperature than any other vegetation type (Snyder et al., 2004). All interaction processes between the environment and canopy follow two fundamental physical principles – the conservation of energy and mass. The absorbed solar energy is consumed in a variety of physical, biological and geochemical processes taking place in forest canopies and in soils beneath them. The radiation input directly drives photosynthesis and stomatal action of the plants, affects the transpiration rates and surface energy balance and thereby temperature and respiration. Forests also extract momentum from the flow, which is highly turbulent over these aerodynamically rough surfaces. The gusty motion of the wind, in turn, is the main transport mechanism of energy, trace gases and aerosol particles between the atmosphere and the surface. The complex structure also affects the environmental conditions within forest canopies: the light intensity and wind speed decrease rapidly within a canopy and become highly variable both in space and in time. Likewise, temperature, humidity and trace gas concentrations may strongly differ from conditions above the forest.

Enhanced greenhouse effect caused by human impacts such as fossil fuel combustion and land use change has perturbed the pre-industrial ‘quasi-equilibrium’ between land and oceanic ecosystems and the atmosphere causing radiative forcing leading to rising global temperature. The atmospheric CO\(_2\) concentration has increased around 100 ppm from the pre-industrial level and global mean temperature risen by 0.74 ± 0.18 °C during the last hundred years (IPCC, 2007). According to climate scenarios, the mean annual temperature in Northern Europe is expected to increase between 2 and 6 °C during 21\(^{th}\) century and the increase is likely to be strongest during winter months lengthening the autumn period and advancing spring recovery (Christensen et al., 2007). The changes in climatic conditions may significantly alter the greenhouse gas budgets and energy and water balances of vegetated ecosystems, forming a direct link between the global climate and biosphere (Chapin et al., 2000; Piao et al., 2008). The explosion of climate awareness and concern of global climate change has lead to growing societal and economic needs for accurate projections for future climate and its influences. Today, large part of our knowledge on the complex multi-scale interactions between the global climate and vegetation is based on models, whose major source of uncertainty can be traced back to the terrestrial biosphere and its processes (Denman et al., 2007). The functioning of boreal coniferous forests and the potential changes in their carbon, water and energy budgets are of particular importance because of their large
extent and presumed sensitivity to climate variability (Chapin et al., 2000; Eugster et al., 2000).

2 Aims

Understanding of ecosystem processes, their variability and drivers, requires versatile long-term measurements at various temporal and spatial scales. This study explores the interplay between biologically active canopy medium, turbulent flow and canopy microenvironment using micrometeorological measurements accompanied by one-dimensional models and ecological and environmental monitoring. The purpose of the present work is to sharpen our understanding of turbulent fluxes\(^1\) of mass and energy, and the canopy processes and environmental factors influencing them in a boreal Scots pine forest.

The specific, although largely retrospective, objectives of this work were:

- To examine the characteristics of turbulent flow within and above a Scots pine forest, close the forest floor in particular, over wide range of diabatic stability conditions. The specific research question was: How does the stability affect the canopy flow? (Paper I)
- Test and validate eddy-covariance (EC) method to measure forest floor net carbon and energy exchange and quantify the forest floor fluxes and their contribution to canopy-scale exchange (Papers II and III)
- To determine the partitioning of aerosol particle dry deposition between the overstory canopy and forest floor (Paper IV)
- To explore the interplay between microenvironment, photosynthesis and transpiration and their vertical variability within the canopy. In particular, we aim to quantify the effect of leaf-level stomatal control description on canopy-scale fluxes (Paper V)
- To describe typical characteristics of energy fluxes and their intra- and inter-annual variability and primary controlling mechanisms at canopy scale (Paper VI).
- To assess the role of environmental conditions, light and temperature in particular, on autumnal carbon balance and its influence on annual carbon budget. The initial hypothesis was: Carbon emissions to atmosphere increase during warm autumns (Paper VII).

In this introductory summary I overview the key interaction processes between vegetation and the atmosphere explored in this thesis. First, I will consider the biological and physical

\(^1\) A term flux is in this study used instead of flux density and represents net transfer of energy of matter through a unit surface per unit time. Likewise, word ecosystem is used in narrow sense as a synonym for a piece of Scots pine forest and soil beneath it but excluding all fauna except soil microbes.
canopy processes related to carbon and water cycles and energy exchange and their role in dynamics of the atmospheric boundary layer. Second, the interactions between canopy medium and flow and the characteristics of turbulent canopy flows are discussed. This gives rise for concept of mass conservation and leads to the fundamentals of turbulent fluxes and eddy-covariance (EC), the state-of-the-art method to measure mass and energy exchange at ecosystem scale. Then, interplay between canopy processes and microenvironment is discussed and integration of point sources to canopy scale is assessed. The role of forest floor on ecosystem-scale mass and energy exchange is considered and their seasonal and interannual variability explored. Finally, the results are critically discussed.

3 Background

3.1 Atmospheric boundary layer and surface energy balance

The amount of solar radiation absorbed at the surface is redistributed based on the first law of thermodynamics, the principle of energy conservation. Setting the reference frame above a horizontally homogenous (see section 5.1) forest, the energy balance equation becomes

\[ R_n = H + LE + G + \sum Q_i , \]  

where net radiation \( (R_n) \) includes short-wave and long-wave radiation budgets. Sensible heat flux \( (H) \) arises from vertical temperature gradient between the surface and the air above and represents the turbulent flux of heat energy from a warm layer to cooler. Latent heat flux \( (LE) \) is related to turbulent flow of water vapor; evaporation of water from (or condensation to) a surface and is thus determined as water flow multiplied by the latent heat of vaporization. In vegetation ecosystems, large part of LE is by transpiration, as discussed later, which plants can strongly affect by opening and closing their stomata. Hence, the response of a plant to its microenvironment affects the energy partitioning at the plants leaves and ambient environment around them (Papers V and VI). Heat flux between soil and atmosphere \( (G) \), driven by vertical temperature differences between the soil layers and the air, occurs mainly by conduction. In addition to radiative and turbulent fluxes observed at the reference level above the canopy, part of the absorbed energy is stored within the system \( (\sum Q_i) \). These storage terms include energy storage to biomass, heating or cooling of the air column between the soil surface and the reference level or changes in its moisture content (latent heat) and transformation of solar energy to sugars in photosynthesis and release in respiration (Paper VI). During winter, snow thermodynamics form also an important component of the energy budget (Ohmura, 2001; Koivusalo and Kokkonen, 2002).
Atmospheric boundary layer (ABL), the lowest $0.5 – 2$ km of the troposphere, is in constant interaction with the surface. The properties of ABL and its structure are influenced by variety of surface – atmosphere interactions, such as momentum transport or energy and mass exchange explored in this thesis. The daily cycle of ABL is highly variable and determined primarily by the energy fluxes from the surface (Figure 1). During a night the energy input received from the sun is zero and negative radiation balance at the surface leads to development of a surface inversion. The stable inversion layer breaks after sunrise when the lower part of ABL is warmed by turbulent heat flux from the surface. As the heating continues, a highly turbulent convective mixed layer develops gradually over the surface destroying the residual layer, a remnant of the mixed layer from the previous day. In the evening, the surface net radiation balance turns negative and the cycle starts again. At the top of the ABL there is entrainment layer through which the exchange between the troposphere and ABL occur. The efficiency depends on the strength of the capping inversion. The lowest $10\%$ of ABL is defined as surface layer, called also as a constant flux layer since the turbulent fluxes are assumed there to be constant with height (Stull, 1988; Foken, 2008). Over rough surfaces, such as forests, this assumption is, however, valid only well above the surface and closest the ground there is a roughness sub-layer (RSL). RSL includes the
canopy sub-layer (CSL) and is the environment where the physical and biological interaction processes between vegetation and the atmosphere take place.

3.2 Carbon and water in a forest

3.2.1 Photosynthesis

“There was land, there was air, there was the distant, hardy sun. Despite immense consumption by the plant world, there was sufficient carbon dioxide in the air, for it was generated by nature. There was water in the ground and minerals plants required. And infinitely far away there was a great ball of fire, the sun, that surrendered its light energy, a sun that shone on good and bad alike, and that rose in the morning and set in the evening.

Pines, from the greatest to the smallest, assimilated. Birches, aspens, rowans and the most insignificant of the grasses assimilated. Through assimilation, the plant kingdom sustained life on the entire planet. The assimilation of carbon dioxide was always the chemical transformation of carbon dioxide and water. Energy was needed in this astonishing process, and this the sun provided as light energy.”

(Veikko Huovinen, Tale of the Forest Folk²)

The micrometeorologist’s view of photosynthesis goes somewhat beyond these lively sentences. Photosynthesis in C3-plants takes place in chloroplasts located in mesophyll cells. The general reaction equation of this complicated chain of processes catalyzed by numerous enzymes is

\[ CO_2 + H_2O + \text{light} \rightarrow CH_2O + O_2, \]  

where CH₂O represents carbohydrates such as sucrose of starch. The substrates for assimilation are CO₂, water and light, which are supplied by ambient environment and the sun. Based on mass conservation, the biochemical demand of CO₂ and simultaneously transpired water vapor must equal the mass diffused through the stomatal pores yielding equations for net CO₂ (\( f_c \)) and water vapor (\( f_e \)) fluxes at leaf scale

\[ f_c = g_s(c_a - c_i) \]

² Veikko Huovinen (1927-2009) was a great finnish humorist, pacifist, satirist – and a graduate forester. During his career he wrote 37 books and several plays. His sharply intellectual and humorous style flowers in novels such as Havukka-Ahon ajattelija and Veitikka, a satiric story of the life of Adolf Hitler. In Tale of the Forest Folk he tells a fascinating story of a naturally regenerating forest and its life cycle from initial forest fire to full-growth old ecosystem. When first published in 1984, Tale of the Forest Folk was a nominate for the Finlandia Prize, the most respected literature award in Finland.
\[ f_c = a_c g_s (e_i - e_a) \approx a_c g_s D, \quad (3) \]

where \( c_a, e_a \) and \( c_i, e_i \) are the ambient and intercellular CO\(_2\) and H\(_2\)O mixing ratios, \( g_s \) the conductance for CO\(_2\) diffusion through the stomatal pores and \( a_c \) (~1.6) the relative diffusivity of water vapor to carbon dioxide in air. When the leaf is well-coupled to the atmosphere (i.e. the leaf temperature is close that of surrounding air), \( e_i - e_a \) can be approximated by the ambient vapor pressure deficit \( (D) \), which is the difference between saturated and ambient vapor pressure.

Figure 2: Photosynthetic light response of two Scots pine shoots in SMEAR II in July 2006. \( P_{\text{max}} \) is light saturated rate, \( \gamma \) the quantum yield (slope of the light response at low PAR) and \( f_d \) dark respiration, the net CO\(_2\) exchange rate \( (f_c) \) when PAR is zero.

The availability of light is often the limiting factor for photosynthesis. In low light, the assimilation rate increases almost linearly but the light response eventually saturates (Figure 2). In ample light, the leaf temperature is important for the saturated assimilation rate since the activity of enzymes such as Rubisco is strongly temperature dependent. At leaf or larger scales the environmental responses of photosynthesis are described by variety of empirical and biochemical models. In Paper V, a biochemical photosynthesis model (Farquhar et al., 1980; Collatz et al., 1991), common in global climate models, was used. In Paper III, the photosynthetic light response was modeled using a Michaelis-Menten -type formulation. The annual cycle of photosynthetic activity is strong in the boreal region; there is intensive production of sugars during the summer but the low sunlight and temperature result to very small, if any, photosynthesis in winter and early spring (Mäkelä et al., 2004; Hari and
Kulmala, 2008). In summer, water availability is the main factor affecting the photosynthetic capacity which determines the light-saturated assimilation rate.

3.2.2 Respiration

About half of the assimilates produced in photosynthesis are directly consumed in maintenance and repair of existing cells and in synthesis of new tissues in different compartments of the plant, e.g. needles, branches and roots (Waring and Running, 1998). This necessary cost of life and growth is called autotrophic respiration, which produces CO$_2$ to the atmosphere. In dark, the whole vertically distributed biomass functions as a carbon source. Eventually, the living cells die and the organic litter and coarse woody detritus serves as a substrate and food for variety of heterotrophic organisms such as bacteria and fungi, which respire CO$_2$ in their metabolism completing the carbon cycle in a boreal forest$^3$. As enzymatic processes, both autotrophic and heterotrophic respiration is strongly temperature dependent (Figure 3) and often approximated with an Arrhenius-type exponential relationship (Lloyd and Taylor, 1994):

$$r_t = r_{i,0}e^{b(1-T/T_0)},$$  (4)

where $r_{i,0}$ is the base respiration rate at selected reference temperature $T_0$ and $b$ an empirical temperature ($T$) sensitivity parameter. In addition to $T$, the heterotrophic respiration depends on the quality of organic carbon in the soil and soil moisture – in dry conditions the decomposition slows down (Kirschbaum, 1995; Pumpanen et al, 2003) and this may happen also in extremely wet soils (Glinski and Stepniewski, 1985). In a forest canopy, the heterotrophic respiration takes primarily place in forest soils. Autotrophic respiration from roots and rhizosphere has a significant contribution on soil respiration; fractions between 62 and 89 % have been reported for boreal forests (Raich and Tufekcioglu, 2000) and 10 – 90 % in vegetation ecosystems in general (Hanson et al., 2000; Raich and Tufekcioglu, 2000). Over the year, the magnitude of autotrophic respiration depends, besides temperature and substrate availability, strongly on photosynthetic production; in Hyytiälä Scots pine forest about 25 % of photosynthates are rapidly released through the roots (Pumpanen et al., 2008). Globally, almost 10 % of atmospheric CO$_2$ circulates through soils annually (Raich and Tufekcioglu, 2000).

On ecosystem scale the amount of carbon assimilated in photosynthesis is called gross-primary production (GPP) and the sum of autotrophic and heterotrophic respiration as total ecosystem respiration (TER). Their sum, the net ecosystem exchange (NEE) of carbon represents the amount of carbon released to atmosphere – when TER exceeds GPP - or fixed per unit time (Figure 4).

$^3$ In forests growing on mineral soils methane emissions are minor compared to respiration. Also the amount of carbon emitted in volatile organic compounds is here neglected.
Figure 3: Temperature response of soil respiration ($R_{\text{soil}}$) in 2006 measured by soil chambers. The average base respiration rate at 10 °C is 2.2 µmol m$^{-2}$ s$^{-1}$ (eq. 4). The clear hysteresis-type behavior shows the importance of other factors such as photosynthetic production and soil moisture controlling $R_{\text{soil}}$. Because of this, both the base rate and temperature sensitivity vary across the season. Intense drought decreased soil respiration during the first three weeks of August (black circles).

3.2.3 Stomatal conductance, transpiration and evaporation

The leaf and needle surface area of the trees were immense. That was as it should be when the objective is to intercept light from space and carbon from the atmosphere. One extremely important task was that of the leaves’ stomata, which were able to open and close. Through the stomata, the carbon dioxide was channeled to the assimilating cell tissues in accordance how the winds delivered it or how it rose from the ground. The production of one kilo of sugar required 800 liters of carbon dioxide, the contents of 2700 cubic meters of ordinary air. That meant a little pine needle had to be busy as a bee gathering nectar from the flowers.

The leaves and their stomata also transpired water and thus attended to the tree’s water resources. Transpiration caused negative pressure in the flow of water leading from roots to crown, and so the leaves’ cell tissues, as it were, sucked water from the roots. Beneath the epidermis of a pine needle, which in cross-section is semicircular in shape, was the assimilative mesophyll. The actual chemical work was performed by specialized chlorophyll a molecules. The needles’ stomata were regulated by guard cells. The stomata closed in the dark as well as during heat waves, when, due to dryness of the earth, the tree suffered from water deficiency.

(Tale of the Forest Folk)
Tiny pores located on plants leaves are called *stomata*. The gas exchange between the ambient environment and the leaf takes mainly place through stomata and the plants can control their aperture by *guard cells* bordering them. At leaf-scale, stomatal conductance is relatively well described by variety models based on the close coupling between the photosynthesis and \( g_s \). As ambient \( D \) increases, stomata tend to respond by partial closure, manifested in approximately exponential decrease of \( g_s \) with \( D \) (Figure 5). The reduction of transpiration occurs to avoid a decline in plant water potential and further physiological damage (Monteith, 1995; Oren et al., 1999). Although the stomata more likely respond to transpiration rate itself than to ambient humidity (Mott and Peak, 1991), the majority of stomatal conductance models utilize the latter because of its appealing simplicity. The most widely spread model spawning from the close relationship between \( f_c \) and \( g_s \) assumes that \( g_s \) varies linearly with the product of \( f_c \) and relative humidity (RH) normalized by CO\(_2\) mixing ratio. The original formulation of this scheme is (Ball et al., 1987):

\[
g_s = \frac{m_i}{c_a - c_{cp}} f_c \times RH + g_0, \tag{5}
\]

where \( g_0 \) is the residual conductance, \( c_a \) ambient CO\(_2\) mixing ratio and \( c_{cp} \) CO\(_2\) compensation point, RH ambient relative humidity and \( m_i \) a species-specific sensitivity parameter (Paper V, Figure 2). An alternative approach to the semi-empirical model above is based on the ‘economics of gas exchange’ and assumes that the regulatory roles of stomata are to autonomously maximize the carbon gains while minimizing water losses (Givnish and Vermeij, 1976; Cowan and Farquhar, 1977; Hari et al., 1986; Katul et al., 2009, 2010a). The models based on optimality hypothesis result to analytical description of stomatal conductance in respect to \( D \) and \( f_c \) (Katul et al. 2009; Paper V) and are compared against the semi-empirical models in Paper V.

Transpiration, flow of water through the plants to the atmosphere, is hence an unavoidable cost of photosynthesis. Evaporating water from liquid to gaseous phase requires energy, primarily provided by the absorbed solar radiation. Consequently, the transpiration modulates the energy balance of a leaf (or canopy) and thereby surface temperature. Transpiration and evaporation (evapotranspiration) can therefore be considered both from the perspective of mass and energy conservation. At canopy scale, evapotranspiration is often modeled using the Penman-Monteith equation (e.g. Monteith and Unsworth, 1990)

\[
LE = \frac{s R_a + \rho c_p D g_u}{s + \gamma (1 + g_u / g_s)}, \tag{2}
\]
where $R_a$ is the available energy ($R_a = R_n - G - \sum Q_i$, W m$^{-2}$), $s$ is the slope of saturation vapor pressure curve (Pa K$^{-1}$), $\gamma$ the psychrometric constant (Pa K$^{-1}$), $\varepsilon = s/\gamma$, $\rho$ the air density (kg m$^{-3}$) and $c_p$ the heat capacity of the air in constant pressure (J kg$^{-1}$ K$^{-1}$). Aerodynamic conductance $g_a$ represents turbulent transport efficiency between the canopy and the atmosphere and $g_s$ is here the effective stomatal conductance over whole foliage (Papers V and VI). Penman-Monteith equation is hence a combination equation which couples the two end-member cases of evapotranspiration; in absence of stomatal regulation (wet canopy, evaporation) LE is controlled only by available energy and temperature while the physiological control of transpiration is accounted through $g_s$ and becomes important when $g_s \ll g_a$. The main components of forest evapotranspiration are shown in Figure 4.

![Figure 4: Schematic view of carbon and water cycles and energy balance in a forest. The net ecosystem exchange (NEE) is a sum of carbon uptake (gross-primary production, GPP) and carbon release (ecosystem respiration, TER). The net radiation ($R_n$) is balanced mainly by sensible ($H$) and latent heat (LE) exchange while ground heat flux ($G$) is small. LE consists of surface evaporation ($E$) and transpiration ($T$). Subscripts $c$, $f$ and $s$ refer to canopy, forest floor and soil, respectively. The dashed horizontal lines represent heights where stand and forest floor net exchange rates were measured by eddy-covariance.](image-url)
4 Turbulent flow within a forest canopy

4.1 Turbulent flows and Reynold’s decomposition

Close the ground the surface friction decelerates the flow and a region of strong vertical wind shear is generated. The shear force exceeds molecular viscous forces between the air layers and the smooth, laminar velocity profile, typical in free troposphere, is perturbed. Instead, the flow profile in surface layer becomes hydrodynamically unstable and kinetic energy from the mean flow is converted to random, irregular and three-dimensional motions. The flow becomes turbulent. Turbulence is created also thermally in convective conditions.

The ASL flows can be interpreted as a superposition of turbulent gusts on smoothly varying steady mean flow, which allows an instantaneous wind speed (\(u_i\)) and scalar (\(s\)) concentration to be represented by Reynold’s decomposition (e.g. Stull, 1988)

\[
\begin{align*}
  u_i(t) &= \bar{u}_i + u'_i, \\
  s(t) &= \bar{s} + s'.
\end{align*}
\]
Here overbar represents time \((t)\) average, the mean part, and prime denotes the turbulent fluctuation along the mean (Figure 6). The averaging time depends on application but generally follows the spectral gap – minimum variability – observed in ABL flows and ranges between tens of minutes to few hours (Stull, 1988).

The chaotic nature of turbulence obliges the use of statistical methods to characterize turbulent flows and turbulent transport. Accordingly, inertial sub-layer (a.k.a. constant flux layer) turbulence is rather well described by similarity theories such as Monin-Obukov theory, in particular in unstable and near-neutral stratification (for a review see Foken, 2006). Over and within rough canopies such as forests, however, ‘niceties’ of similarity theory break down because the flow statistics are significantly modulated by the roughness elements leading to generation of intense semi-organized turbulence that is no longer in local equilibrium (Kaimal and Finningan, 1994; Raupach et al., 1996; Finnigan, 2000).

![Figure 6: Turbulent time series of vertical wind \((w)\) and temperature \((T)\) measured on a clear sunny summer afternoon by a sonic anemometer at 23.3 m height, abound 8 m above a pine forest. The overbar represents time average and prime the instantaneous turbulent fluctuation around the mean (eq. 7). The mean values are denoted by dashed horizontal lines and fluctuating parts, at few occasions, by arrows. Note the ramp-like behavior of temperature signal and correlation with \(w'\).](image-url)
4.2 Canopy turbulence

“But the most beautiful, the most profound, the most soothing was the way in which the wind passed through the forest tresses. Millions of needles and leaves dipped, danced, rustled, whispered, soughed. The giant fur coat of the forest unfurled, flared; the branches of a weeping birch floated like a sheet, and aspen leaves fluttered. Further down, bushes and saplings shifted, gleaming in the light or bending, ghost-like, in the fog. A juniper branch swept needles and crumbs of lichen over the sand as it passed and brought them back again on its return. A bent reed drew its endless circle in the snow.”

*(Tale of the Forest Folk)*

In *Paper I*, we analyzed the characteristics of turbulence inside and above a Scots pine forest in detail. The main target of the paper was to explore the effect of diabatic stability to canopy flows — an aim that was assessed by conditionally sampling the first and higher-order velocity statistics to four stability classes based on stratification above the canopy (*Paper I*, Figure 2).

Figure 7 shows normalized vertical profiles of mean wind speed ($U$), momentum flux ($u'w'$) and standard deviations of streamwise and vertical wind components ($\sigma_u, \sigma_w$) in near-neutral conditions superimposed to data from several other vegetation canopies (Katul et al., 2004a) and a flume experiment where the canopy consisted of vertical rods (Poggi et al, 2004). Several characteristic features of canopy turbulence can be recognized: 1) the wind profile is inflected around the canopy top ($z = h$); the velocity profile above the canopy follows logarithmic relationship, standard for boundary layer flows (not shown), but decays roughly exponentially inside the canopy (Finnigan, 2000). The maximum shear ($dU/dz$) occurs around the canopy top and a weak secondary wind maximum can exist below the canopy. In absence of dense understory vegetation a second logarithmic layer is observed immediately above the forest floor. 2) Majority of the momentum is absorbed as aerodynamic drag ($F_d(z) \propto C_d(z)U(z)^2a(z)$, where $C_d(z)$ and $a(z)$ are local drag coefficient and leaf-area density) in upper layers of the canopy and hence $u'w'$ is almost zero in lower canopy layers.

3) The standard deviations are highly inhomogeneous with height but especially $\sigma_u/u_s$, remains large all the way down the forest floor. This indicates that there exists intense turbulence throughout the CSL but in lower canopy it is inefficient in terms of momentum transport. The origin of this inactive eddy motion is likely to be in upper layers of the canopy where the flow instabilities are produced by the strong shear and these eddies then lose their momentum transporting efficiency to the canopy drag to become inactive in trunk space. 4) The velocity statistics are highly skewed in the canopy crown but become more symmetric again in trunk-space (*Paper I*, Figure 4). Large positive and negative skewness ($Sk = \bar{u'}^3/\sigma^3$) of horizontal and vertical wind components, respectively, is consistent with the importance of energetic downward moving gusts penetrating the canopy and reaching the forest floor (Raupach et al., 1996; Finnigan, 2000; *Paper I*). Likewise, high kurtosis
observed in plant canopies is caused by the intermittency of the energetic coherent motions, also verified by the quadrant-hole analysis (Paper I, Figure 6; Paper IV, Table 2).

The observations in Figure 7 and in plant canopies in general are rather well explained by analogy between canopy and plane mixing-layer flows (Raupach et al., 1996; Finnigan, 2000). The strong vertical wind shear and inflection point at canopy top resembles a plane mixing layer where two horizontal airstreams having large velocity difference are initially separated by a horizontal plate and merge after the trailing edge of the plate. The flow around the free shear layer becomes hydrodynamically instable and hence any perturbation tends to grow. In canopy flows, the initial perturbations are gusts of wind. They raise the shear at canopy top over a critical threshold value at which Kelvin-Helmholtz – type instabilities can emerge, grow in proportion to magnitude of the shear and finally break into fully developed turbulence (Raupach et al., 1996; see Figure 12 in Finnigan, 2000). The dominating structures in canopy turbulence, called coherent eddies, are therefore remnants of the primary Kelvin-Helmholz –waves. Hence, the characteristic vertical dimension of the coherent eddies depend on the shear length scale \( L_s \) that is primarily a function of canopy height and aerodynamic drag (Finnigan, 2000). The streamwise separation (the distance or time between the coherent eddies in the flow), on the other hand, has been found in wide range of canopies to cluster around 8.1 \( L_s \) (Raupach et al., 1996) and tends to decrease in stable conditions (Brunet and Irvine, 2000).

In relative open canopied forests such as Hyytiälä site, diabatic stability inside the forest follows qualitatively the stability regime above the canopy. In Paper I we found that the flow statistics agreed the mixing-layer analogy in unstable to weakly stable conditions and the first-order modulations of canopy turbulence were explained by the stability conditions above the canopy. In strongly stable stratification, however, the shear stress attenuated and correlation coefficient between \( u' \) and \( w' \) decreased faster compared to near-neutral or unstable regime, in line with Shaw et al. (1988). In addition, the mean wind profile was significantly altered in trunk-space where the local drag was smallest due to low plant area density leading to a distinct secondary maximum and enhanced \( \sigma_u/u \) and \( \sigma_w/u \) (Paper I, Figure 3). The likely reason for the strong secondary maximum is the sloping topography of the site that induces horizontal pressure gradient to the flow (Shaw, 1977; Katul et al., 2010b) and promotes nocturnal drainage flows that may bias the nighttime EC measurements of mass and energy exchange conducted either above the canopy (Papers V, VI and VII) or in trunk-space (Papers II, III and IV) in stable nighttime conditions.

---

4 See a visualisation of Kelvin-Helmholtz –instability: [http://www.youtube.com/watch?v=CL7s8h7mtPE](http://www.youtube.com/watch?v=CL7s8h7mtPE)
Figure 7: Ensemble averaged flow statistics collected in range of canopies and normalized by friction velocity ($u^*$) at the canopy top. The results from Paper I (near-neutral stratification) are superimposed and shown by black circles. The figure is re-drawn from Katul et al. (2010c) and the sites are described in Katul et al. (2004a). Leaf area of Hyytiälä-site is shown in Figure 12.

4.3 Turbulent kinetic energy and spectra

A unique feature of CSL is that the canopy interacts with the flow throughout its depth and the turbulence is not in local equilibrium as in surface layer. Figure 8 illustrates the creation and destruction of turbulent kinetic energy (TKE) in plant canopies. The mean background flow ($U$) loses kinetic energy to TKE when the large coherent structures are created in the shear layer. In addition, TKE is created in turbulent wakes forming behind the tree trunks, branches and needles; energy from mean flow is converted to turbulence in spatial scales characteristic of the roughness elements ($d_r$). Similarly to mean flow, the large eddies lose their momentum by form and viscous drag on the canopy elements, shown as ‘spectral short cut’ in Figure 8. The wake production and short-circuiting of eddy cascade are strongest at upper canopy where the form drag is greatest and turbulence in lower canopy is maintained largely by transport from higher layers (Figure 8). In Paper I, we showed how the power spectra of wind components and temperature are modulated when descending from above the canopy towards the forest floor (Paper I, Figure 9). Above the canopy the power spectra followed the surface layer model (Kaimal et al., 1972; Rannik et al., 1998) with -2/3 slope at inertial sub-range. At canopy top and in trunk-space in particular the spectra were distorted
due to the drag imposed by the canopy elements and horizontal wind components decayed steeper than -2/3 slope at frequencies corresponding the low-frequency end of inertial subrange. At higher frequencies, increase of power spectral densities was observed, consistent with the short-circuiting and wake/waving production shown schematically in Figure 8. However, the multiplicity of length scales of canopy elements (trunk diameter, cone diameter, branches, shoots, needles) makes it hard to discern a unique wake production length scale. Contrary to horizontal velocity components, the spectral peak of $w'$ broadened and shifted to higher frequencies in lower trunk-space because proximity of surface restricts the vertical eddy size. At vicinity of the ground ($z \approx 20$ cm) the spectral peak was shifted to significantly higher frequencies indicating dominance of very small eddies. In Paper I, two alternative hypotheses were drawn to explain this behavior: First, a shallow boundary layer characterized by the near-logarithmic wind profile forms above the forest floor (Paper I, Figure 3) and hence the classical boundary layer mixing length $\sim k_v z$ (~13cm here) resembles the dominating eddy size. Second, there is possibility that the shift in peak frequency is caused by shedding of von Karman vortexes behind the tree trunks. The latter mechanism has been observed both in an artificial canopy consisting of rods (Poggi et al., 2004; 2006) and in forests (Baldocchi and Meyers, 1988; Cava and Katul, 2008). It is notable that scalar power spectra remain less affected inside the canopy (Paper I, Figure 9; Paper IV, Figure 2).

Figure 8: Schematics of turbulent kinetic energy budget in roughness sub-layer (RSL) and its implications on velocity power spectra in wave number ($k$) space. In upper left corner black arrows illustrate interactions between mean flow and canopy that create TKE into scales determined by the shear length scale ($\Lambda_u$) and characteristic length of roughness elements ($d_r$). Red arrow indicates bypass of energy cascade from large shear-generated eddies to smaller ones as a result of wake production. Hence, the classical inertial sub-range (slope $k^{-5/3}$) does not exist inside canopy. Drawn after Kaimal and Finnigan (1994) and Finnigan (2000).
5 Measuring matter and energy flows between ecosystem and the atmosphere

Exchange of mass and energy between an ecosystem and the atmosphere is measured by different methods depending on the scale of interest. Chamber methods are often used to study processes such as photosynthetic light response, dark respiration or soil CO$_2$ efflux and their environmental dependencies at small scales (i.e. at shoot scale or <1 m$^2$ of soil or trunk surface). At ecosystem scale, i.e. at whole-forest scale, micrometeorological eddy-covariance technique has emerged as a standard tool to monitor the turbulent fluxes; the flux tower network spans over the globe and contains nowadays more than 500 sites (Baldocchi, 2008; www.fluxnet.ornl.gov).

Within a forest ecosystem momentum, heat and trace gases have complex source/sink distributions which vary both in time and space – as does the flow field. Hence, the simple time averaging done for turbulent ASL flows has to be replaced by a time – volume average in CSL (Raupach and Shaw, 1982). From experimental point of view, the breakdown of homogeneity is challenging and calls for horizontally arrayed turbulence measurements to collect both the temporal and spatial variability. In practice this requirement is circumvented by ensemble averaging CSL measurements collected at one point in space over extensive periods of time. This is because ergodicity hypothesis (in ‘weak’ sense) states that the time average should converge towards space – time average when the averaging period is sufficiently long to cover the full range of wind directions (Katul et al., 2004b). This assumption was made in particular in Paper I by analyzing the ensemble averaged turbulence statistics.

5.1 Mass balance in turbulent roughness sub-layer flows

In turbulent RSL flows the conservation of substance $s$ within a given volume is given by

$$\frac{\partial \bar{s}}{\partial t} = \sum_{i=1}^{3} u_i \frac{\partial \bar{s}}{\partial x_i} + \sum_{i=1}^{3} \frac{\partial u_i}{\partial x_i} \bar{s} + \sum S_s,$$

where overbar represents the space – time average and molecular and dispersive terms, spawning from spatial correlations within the volume (Raupach and Shaw, 1982), are neglected. The notations $u_i$ and $x_i$ have their standard meteorological forms: $u_1 = u$, $u_2 = v$, $u_3 = w$ and $x_1 = x$, $x_2 = y$, $x_3 = z$. Assuming stationary (no change in time) conditions the time derivative vanishes and horizontally homogeneous (no change in x and y direction) source/sink ($S_s$) distribution, flat topography and incompressible flow, the advection terms
and horizontal turbulent fluxes can be neglected. With these simplifying assumptions, eq. 8 reduces to

$$0 = \frac{\partial \overline{w's'}}{\partial z} + \sum S_s(z)$$

(9)

and integrating with respect to z yields

$$\overline{w's'}(z_{\text{ref}}) = -\int_{z=0}^{z_{\text{ref}}} S_s(z).$$

(10)

Hence, in ideal conditions defined above, the turbulent vertical flux ($\overline{w's'}$) per unit area at the upper boundary ($z_{\text{ref}}$), equals the sum of all sources/sinks within the volume (Figure 9). Origin of turbulent flux can be intuitively understood by considering the continuous eddy motion across the reference level, shown at the right edge of Figure 9. First, note that mean concentration, $\overline{C_z}$, decreases with height and a downward moving gust ($w' < 0$) carries an air parcel with less than average concentration ($s' < 0$) downwards. Similarly, upward eddy motions ($w' > 0$) tend to continuously transport high-concentration air ($s' > 0$) from deeper layers to the reference height. This eddy motion is continuous and as a consequence there is net flow of $s$ through $z_{\text{ref}}$ per unit time. Hence, by definition, $\overline{w's'}$ is the covariance between wind speed fluctuations and corresponding perturbations in a scalar concentration. Moreover, the large coherent eddies creating strong $|w'|$ transport $s$ further away and therefore create larger $|s'|$ than smaller scale turbulence which only locally mixes the air, approximation known as Prandtl’s mixing length hypothesis (see e.g. Arya, 2001). In forest canopies the concentration profiles can, however, be complex. For instance CO$_2$ may have a local minimum in crown layer where intense assimilation takes place in daytime and a maximum close the ground where mixing is weak and CO$_2$ is produced by soil respiration more than taken up by the ground vegetation (Paper V, Figure 5). On the other hand, the large intermittent coherent structures, ranging from tens to hundred of meters in size, are responsible for majority of the turbulent transport (Raupach and Thom, 1981; Finnigan, 2000; Paper I, Figure 6; Paper IV, Table 2). The large eddies create strong, ‘ramp-like’, fluctuations in scalar time series, as indicated in Figure 6. Because the length scale of the transporting eddies is of the same order or larger than the length scale over which the concentration varies, the gradient-diffusion analogy$^5$ breaks down in CSL and transport can be counter the local gradient (Kaimal and Finnigan, 1994). Nevertheless, for simplicity ‘K-theory’ is often utilized to approximate turbulent transport also in plant canopies, as done in Paper V.

---

$^5$ The gradient-diffusion approximation for turbulent transfer: $\overline{w's'} = -K_s \frac{\partial \overline{s}}{\partial z}$, where $K_s$ is the eddy diffusivity (transport coefficient), analogous to molecular diffusivity/conductivity but several orders of magnitude larger.
5.2 Eddy-covariance

Equation 10 states that in stationary, horizontally homogeneous conditions the net exchange of mass (e.g. CO$_2$ and H$_2$O) and energy (heat, momentum) between ecosystem and the atmosphere occurs only as a vertical turbulent flux. This is the core assumption of EC-method, which is the only direct technique to measure the turbulent fluxes. In EC the three wind components and virtual temperature are measured at high frequency, typically 10 – 20 Hz, using a sonic anemometer (Figure 10). Simultaneously, the high-frequency fluctuations of scalar quantities in the air are measured nearby using appropriate analyzers. The mixing ratios of CO$_2$ and H$_2$O are detected by fast response open- or closed-path infra-red absorption gas-analyzers and fluctuations in aerosol particle number concentrations by a condensation particle counter (CPC). The turbulent vertical fluxes of momentum (\(\overline{w'u'}\)), sensible and latent heat, CO$_2$ and aerosol particle number fluxes are then calculated as a covariance between the vertical wind speed fluctuations (\(w'\)) and respective scalar fluctuation (\(s'\)) over a desired averaging time (\(\frac{1}{2}\) h in this thesis). The EC measurement made at single location above or within a forest represents average conditions over extensive upwind source area (Figure 9). The footprint size varies with measurement height, upwind topography, wind speed and surface layer stability. In near-neutral conditions 80 % of the scalar fluxes measured at 23 m height (7 – 10 m above treetops) at SMEAR II-station originate between 200 and 300 m upwind from the measurement mast (Sogachev et al., 2004). When the surface layer is stably stratified, as in night time, the source area is larger than in near-neutral because the turbulent exchange is weaker while the case is opposite in unstable conditions.

Although the basic principle of EC is simple, there are several technical and methodological challenges. For instance, inadequate frequency response of the sonic anemometer and gas analyzers cause systematic underestimation of the contribution of smallest scale turbulence. Similarly, the low-frequency contribution of the flux may be missed because of the choice of averaging time and thus both effects have to be accounted using co-spectral correction methods (Moore, 1986; Aubinet et al., 2000; Massman and Clement, 2004). The methodological problems include, for example, non-ideal measurement sites where horizontal homogeneity is limited. This may create directional differences in measured fluxes and complicate the interpretation of ecosystem responses. In addition, vertical and horizontal advection and storage below the measurement height, which cannot be detected by EC, may become important component of the mass balance in stable conditions during night time (e.g. Aubinet, 2008). In these conditions the measured flux does not represent the net biological, physical or chemical sinks and sources as desired. Also, there is no uniform methodology to conduct the EC measurements or post-process, quality screen and gap-fill the data despite recent advances (Lee et al., 2004). Regardless the caveats of EC, its undisputed benefit is that it is the only direct method to detect turbulent whole-ecosystem – atmosphere fluxes. Therefore, it suits especially for detecting whole-ecosystem responses but is also successfully used for estimating annual and seasonal balances (e.g. Baldocchi, 2008; Papers VI and VII).
Since micrometeorology considers the mass and energy balance from atmospheric perspective the fluxes are normally defined positive when directed away from the surface.

Figure 9: The principle of eddy-covariance is based on mass balance approach. In horizontally homogenous and stationary conditions the turbulent vertical flux at upper edge of the box \((z_{ref})\) should equal the integral over all sources and sinks, \(S(z)\), within the studied volume (eq. 10). Eddies create correlated variations in vertical wind speed \((w')\) and scalar concentration \((s')\) and thus efficiently transport mass and energy in vertical direction. Schematic concentration profile \(C_z(z)\) is shown in right.

**Paper II** focused on validating long-term use of EC method to measure forest floor contribution on canopy scale \(\text{CO}_2\) and energy fluxes. We found that EC method can indeed be used in a trunk-space of a relatively open forest given the stationarity requirements are fulfilled and the turbulent mixing inside the stand is strong enough. We observed that below a given threshold value of standard deviation of vertical wind speed \((\sigma_w)\), irregular variability of \(\text{CO}_2\) flux increased significantly (**Paper II**, Figure 2). This typically occurs in calm nighttime conditions, during which the turbulence is weak, intermittent and highly unstationary. When the mixing is stronger, however, the trunk-space flux measurements behave well and represent the net exchange between the forest floor (understory and soil) and the air in trunk-space (Misson et al., 2007). In **Paper II** the 80 % footprint for sub-canopy EC measurements was estimated to be around 50 m but recent calculations using a Lagrangian footprint model (Rannik et al., 2003), parameterized with turbulence profiles given in **Paper**
I, indicated that the source area for ground sources is significantly larger, between 150 – 200 m (Rannik and Launiainen, unpublished results). The discrepancy is mainly due to different parameterization of $\sigma_w$ and Lagrangian time scale close the forest floor.

While EC gives a direct measure of the net exchange between the ecosystem and the atmosphere averaged over large source area, it cannot distinguish between different layers of the canopy or between sub-processes such as photosynthesis and different components of respiration. Hence, for instance GPP and TER have to be separated from NEE using e.g. temperature regressions of night time NEE extrapolated to daytime conditions (Markkanen et al., 2001; Reichstein et al., 2005; Kolari et al, 2009; Paper VII).

Figure 10: Measurement devices at SMEAR II. Top: Main mast where canopy scale fluxes and concentrations are measured; the 3D wind field is measured by sonic anemometer. Bottom: Chambers to monitor shoot gas exchange and soil CO$_2$ and H$_2$O fluxes.
5.3 Chambers

Contrary to EC, chambers are an indirect method to determine gas exchange. The studied object, i.e. one shoot or small fraction of forest floor, is enclosed inside a chamber and the effect of the object on its environment is monitored (Figure 10). To estimate $\text{CO}_2$ and $\text{H}_2\text{O}$ fluxes, the rate of change of respective mixing ratio within the chamber is recorded over the closure time and the exchange rates are calculated based on mass balance. Hence, the chamber method gives the exchange rate of a substance per area or mass enclosed in the chamber, which is then upscaled per unit surface or ground area. As small-scale measurements, the chambers suit well for process studies and for determining environmental responses (Papers III and V). Upscaling to ecosystem level, however, requires accurate data on biomass distribution and appropriate models to describe the local microenvironment – primarily radiation, humidity and temperature – each canopy element is exposed to.

5.4 SMEAR II - site

All the research papers included in this thesis use micrometeorological and ecological measurements made at SMEAR II - research station. The measurements and methodologies are described in respective research papers and therefore only a short overview of the site is given here. SMEAR II is located next to the Hyytiälä forest station of the University of Helsinki in southern Finland (61° 51’N, 24° 17’E, 181 m above sea level). The site is relatively homogenous boreal Scots pine stand ($\text{Pinus sylvestris}$ L.) sown in 1962. The forest belongs to the Vaccinium site type according to the Finnish forest site type classification (Cajander, 1926). The study site represents typical commercially managed pine forest in Finland. The mean canopy height has increased from 13 m in 1997 to 16 m in 2008. In 2001, the stem density was ~1800 ha$^{-1}$ but between January and March 2002 most of the stand was thinned to density of 1000 – 1200 ha$^{-1}$, resulting in about 27 % reduction in tree biomass and foliage area within the closest 100 m on the southern sector (Vesala et al., 2005; Ilvesniemi et al. 2010)$^6$. Consequently, total (two-sided) leaf area index (LAI) dropped from 8 to 6 m$^2$ m$^{-2}$ (annual average) but the earlier level was rapidly re-established in a few years. The forest floor vegetation is dominated by lingonberry ($\text{Vaccinium vitis-idaea}$), blueberry ($\text{Vaccinium myrtillus}$) and mosses, mainly $\text{Pleurozium schreberi}$ and $\text{Dicranum polysetum}$. In 2005, 30 % of the dry biomass was lingonberry, 19 % blueberry and 35 % mosses (Paper III); total LAI of the shrubs has been estimated to be about 0.5 m$^2$ m$^{-2}$ and the mosses 1.0 m$^2$ m$^{-2}$. The mosses have total percentage cover of about 60 % overlying a 5 cm organic humus layer (Kolari et al., 2006). The soil is a Haplic podzol on glacial till. From 1970 to 2000, the mean annual temperature was +3.3 °C and precipitation 713 mm. The advantage of SMEAR II – research station is that it is designed for measuring ecosystem – atmosphere exchange continuously at various scales and covering all necessary compartments of the ecosystem and its environment (Hari and Kulmala, 2005; Hari and Kulmala, 2008).

---

$^6$ The reported ~28% reduction in biomass represents the thinned areas only. This value should be scaled over the full EC footprint to get “effective” numbers for EC studies.
6 Overview of the results

The research papers included in this thesis consider some of the most fundamental interaction processes between the atmosphere and a forest. Since the specifics of canopy turbulence (Paper I), prerequisite for understanding the turbulent exchange, were previously introduced, this section aims only to give an introductory overview of the results of Papers II – VII.

6.1 Aerosol dry deposition

The process by which aerosol particles collect or deposit themselves on solid surfaces, decreasing the concentration of airborne particles is called deposition. It can be divided into two sub-processes: dry and wet deposition. Dry deposition is transport of particulate matter or gases from the atmosphere onto surfaces in absence of precipitation. Dry deposition is one mechanism which affects the mass and number distribution of atmospheric aerosol particles and hence influences the magnitude of direct and indirect climate effects of aerosols (IPCC, 2007), visibility and air quality issues and health impacts. The particle dry deposition can be intuitively thought as a chain of processes taking place partly in series and in parallel (Seinfeld and Pandis, 1997; Pryor et al., 2008): First, the turbulent flow transports (sub-micron) particles through the ASL and CSL to a thin quasi-laminar sub-layer adjacent to all still surfaces. Both thickness and stationarity of quasi-laminar sub-layer and turbulent transport efficiency depend on turbulence properties such as its intensity. In addition to turbulent transport, the gravitational settling becomes important for particles larger than a few micrometers in diameter. Second, the transport across the few millimeters thick quasi-laminar sub-layer occurs either by Brownian diffusion7 (smallest particles, \(d_p < 0.5 \mu m\)), by interception – particles moving with mean air flow sufficiently close the surface so they touch it – or by inertial impaction, in which the particles hit the surface because they cannot follow the curved streamlines because of their inertia (Figure 11). Third, the characteristics of the surface and depositing particle finally determine whether deposition occurs or if the particle bounces off from the surface (Seinfeld and Pandis, 1997). The particle number flux \((F_p)\) from the atmosphere to the surface depends naturally on particle concentration \((\bar{C}_p)\) and to study and model the deposition processes a concentration-normalized representation for particle deposition is desirable. That is achieved by size-dependent deposition velocity \((v_d)\)

\[
v_d = -\frac{F_p}{\bar{C}_p}, \tag{11}
\]

which accommodates all processes occurring along the deposition pathway.

---

7 Visualization of Brownian diffusion: http://www.youtube.com/watch?v=2Vdjin734gE&feature=related
In Paper IV the partitioning of aerosol dry deposition to canopy and forest floor beneath it, a key gap in present knowledge (Pryor et al., 2008), was assessed using two-layer EC measurements using a condensation particle counter (CPC) for detecting the turbulent fluctuations in particle number concentration. The measurements were made in Hyytiälä in second half or March, 2003, a period characterized by daily particle formation events. As a consequence of the condensation and coagulation leading to particle growth, geometric mean diameter had distinct diurnal cycle with minimum around 10 nm in early afternoon and maximum around 40 nm in early morning (Paper IV, Figure 11) and total number concentrations between 2500 and 6000 particles per cubic centimeter. In Paper IV we showed that the particle number flux was dominated by the sweep-ejection cycle both above the canopy and in trunk-space. The large eddies, ranging from tens to hundred meters in size assuming hypothesis of frozen turbulence (Taylor, 1921), created strong excursions in particle concentrations: the strong downdrafts (gusts) brought particle enriched air towards the ground while the compensating, longer-lasting but weaker, updrafts (ejections) carried particle depleted air. Above the canopy the sweeps contributed about equally to particle and heat transport while the ejections were more important for particles. Beneath the canopy the situation was qualitatively similar but also interactive quadrants, i.e. cases when downdrafts are associated with lower $\overline{C_p}$ or vice versa, had larger effect on net transport (Paper IV, Figure 11).
Table 2). To conclude, aerosol dry deposition was governed by the same semi-organized turbulence field than momentum transport and exchange of other scalars such as heat and CO$_2$, also shown in Pryor et al. (2007).

We explicitly showed in Paper IV, to my best knowledge for the first time, the importance of forest floor beneath the canopy on dry deposition and found that the forest floor vegetation accounts for between 10 and 35 % of the total dry deposition of particles within size range 10 – 30 nm. Moreover, the fraction seemed to be dependent on turbulence intensity: Increasing turbulence enhanced the deposition into the needles and in strongly turbulent conditions (characterized by friction velocity ($u^*$) in Paper IV) the forest floor contribution becomes almost negligible (Paper IV, Figure 12). However, in a study taking advantage of long-term two-layer particle flux measurements at SMEAR II – site, we did not observe any dependency of floor/canopy partitioning on turbulence intensity or particle Reynolds number (Katul et al, 2010b). Whether a specific property of the short-term measurement period in Paper IV or a more general finding, the relative increase of foliage deposition in strongly turbulent conditions may imply that the vegetation collection efficiency increases in these conditions, possibly because: 1) the quasi-laminar sub-layers pinned at the needles get thinner and less stationary, or 2) by enhanced turbo-phoresis. Turbo-phoresis refers to the tendency of particles to migrate in the direction of decreasing turbulent energy. A qualitative visualization of this effect can be seen in rapids where floating litter concentrates on the lull regions between streams and vortices. In an inhomogeneous flow characterized by large gradients in the vertical velocity variance, as is the case within forest canopies, turbo-phoresis is expected to enhance particle deposition rate onto the surface (e.g. Caporaloni et al., 1975; Young and Leeming, 1997). Recently, we used a layer-resolving model and showed that turbo-phoresis increases $v_d$ of 0.1 – 2 µm particles by almost order of magnitude in upper half of the canopy where the foliage is concentrated (Katul et al., 2010b). It was also shown that inclusion of turbo-phoresis in a multi-layer model produced $v_d - d_p$ relationship closer what has been observed over forests (see Pryor et al. 2008 for a review). In addition, the shape of vertical leaf area profile has strong influence on $v_d$: canopies that have large leaf area at canopy top are most efficient to capture particles. This is because the vegetation collection mechanisms for aerosol particles are in general proportional to the product of leaf-area density, $a(z)$, and Reynolds stress. Hence, in canopies where the maximum $a(z)$ occurs in regions of small momentum flux, a large fraction of foliage becomes “inefficient” as a depositing surface (Katul et al., 2010c). Because of this, the leaf-area density profile seems to have greater importance on $v_d$ than the total LAI – especially in dense canopies.

6.2 Variations in microenvironment, photosynthesis and transpiration in the canopy

Within a forest the environmental conditions, light regime and wind in particular, differ substantially from the conditions above the stand. The needles, branches and trunks absorb radiation; its intensity rapidly decays when descending into the foliage (Figure 12). In a forest canopy the sun and shade patches alternate and light regime varies constantly below the
fluttering leaves. As a first approximation, the radiation decay within the foliage can be described by Lambert-Beer law of extinction in a homogenous porous medium (e.g. Campbell and Norman, 1998, Paper V). Thus, the average intensity at each height $z$ is determined by the amount of leaf area above $z$, solar elevation and quality of light (direct / diffuse). Also the wind is rapidly decelerated by the foliage (Figures 7 and 12) but the relatively calm flow inside a forest is frequently broken by gusts, which ventilate the canopy air space and smooth the vertical and horizontal temperature, moisture and CO$_2$ gradients developed during calm periods. The sinks and sources naturally affect concentration gradients of trace gases and temperature within a forest. During daytime, CO$_2$ mixing ratio typically gets a local minimum and H$_2$O a local maximum inside the upper canopy where carbon assimilation and transpiration are strongest. The mixing ratios peak at the ground because there respiration exceeds photosynthesis and thus forest floor acts as a CO$_2$ source as it does for water vapor (Paper V, Figure 5). In open-canopied, well-ventilated stands such as Hyytiälä –site, temperature gradient within the forest are rather weak except in very stable conditions (Paper I, Figure 3).

Variety of biological, chemical and physical processes taking place at each canopy element depend on the microclimate the element is exposed to. For the biological processes, photosynthesis in particular, the vertical changes in temperature and air humidity are of minor importance compared to light variation. In Paper V, we studied how various formulations of leaf-level stomatal regulation influence vertical sink/source profiles and up-scaled canopy fluxes of CO$_2$ and H$_2$O. A multi-layer model (MLM) was built by assuming that each needle operates its stomata autonomously depending on the layer-averaged microclimate it is exposed to but that the sensitivity to the microclimatic fluctuations remains similar across the stand. Four different formulations for the leaf stomatal conductance ($g_s$) were combined with a leaf-level photosynthetic demand function (Farquhar et al., 1980), a layer-resolving light attenuation model (Campbell and Norman, 1998), and a turbulent gradient diffusion scheme for scalar fluxes within the canopy. The stomatal control models, two variants of commonly used Ball-Berry scheme (eq. 5) and two models based on optimality hypothesis (Katul et al. 2009), were parameterized against same shoot gas exchange dataset collected at upper part of the crown (Paper V, Figure 2).

The MLM predicted rapid decrease of photosynthetic rate, $g_s$, and transpiration towards the forest floor, as expected taken the dominant role of radiation driving the carbon and water fluxes (Paper V, Figure 5 and 9). When the ambient $D$ is high and there is ample light, the needles tend to regulate excess water loss by transpiration by closing their stomata. This causes $g_s$ and assimilation rate to decrease in summer afternoons. Based on model predictions in Paper V, the stomatal regulation has larger effect in upper canopy where the photosynthesis is light-saturated. The fraction of sunlit foliage decreases rapidly in the crown and the transition from primarily temperature to light limited assimilation occurs accordingly. In the deeper layers, the diurnal pattern of $g_s$ becomes more ‘symmetrical’ since any alteration in light conditions creates a linear change in assimilation and the importance of stomatal control on regulating assimilation diminishes. In the lower half of the canopy the
effects of stomatal regulation are hardly visible (Paper V, Figure 9). Accordingly, the water use efficiency (amount of CO$_2$ assimilated per unit of transpired H$_2$O) decreases in the lower canopy (Paper V, Figure 5) and, hence, in terms of water use, assimilating CO$_2$ becomes less economical. On canopy scale this means that carbon sink and water vapor source profiles do not merge and the lower layers have larger contribution to the latter. Also the ratio of leaf internal to external CO$_2$ concentration increases when descending deeper into the canopy because photosynthesis decreases faster with height than $g_s$ (Ellsworth, 1999 and 2000; Niinemets et al., 2004; Paper V, Figure 5 and 9).

Figure 12: a) Leaf-area density profile, $a(z)$, and radiation attenuation (grey line) inside the canopy. The assimilation rate ($A_m$ dashed line) is rapidly reduced inside the canopy. b) The vertical CO$_2$ sink/source distribution, $S_c(z)$, becomes unsymmetrical with respect to $a(z)$. c) Integrating $S_c(z)$ from the ground upwards gives net CO$_2$ flux ($F_c$) and d) water vapor flux profile (here in terms of latent heat flux, LE) at each height. The data and modeled profiles ($g_s$ – scheme according to Leuning (1995)) in b – d are from Paper V and represent daytime (08 – 18 local time) conditions during a summer. Negative values represent net uptake and positive net release of CO$_2$ or H$_2$O.
6.3 Upscaling to canopy level

Upscaling CO$_2$ and H$_2$O fluxes from canopy element scale to ecosystem (stand) level, as done in Paper V, merges to equation 10: at each height the upscaled flux represents the net of sinks and sources beneath $z$ (Figure 9). This allows direct comparison of predicted CO$_2$ and water vapor fluxes against the multi-level EC measurements (Papers I, II and V). Since the turbulent transport scheme was included in MLM, the mean scalar concentration profile measurements can be used as well. In this respect the study presented in Paper V is rather elegant – the spatial scale the model is parameterized is fully independent on the scale it is validated, a desired condition seldom fulfilled in ecosystem – atmosphere upscaling studies. Paper V also illustrates explicitly how different formulations of a single phenomenon, each of them equally valid at leaf-scale, can manifest them at a canopy scale while everything else in the model is kept constant. Our comparison of upscaled canopy level fluxes revealed that the representation of the leaf-level stomatal control alone can have about ~15 % influence on canopy scale CO$_2$ and ~30 % influence on water fluxes, not a small fraction given that their parameters where inferred every day from the shoot chamber measurements. Concurrently, the vertical profiles indicate that the contribution of a single layer to the upscaled fluxes differ somewhat among the $g_s$-schemes (Paper V, Figure 5). All four models studied in Paper V predicted the measured net carbon exchange to within 15 % and latent heat fluxes to within 25 % accuracy (Paper V, Figure 6 – 7). Besides, within each $g_s$ model, the CO$_2$ fluxes were insensitive to the model parameter variability but the transpiration rate was notably more affected.

Upscaling the processes and fluxes to canopy level leads to ‘big-leaf’ representation of the canopy, a common approach used in various land surface schemes applied in climate, weather prediction and hydrological models (e.g. Sellers et al., 1996, Noilhan and Planton, 1989; Wigmosta et al., 1994). In ‘big-leaf’ models the whole canopy is considered as a single layer with effective physical and physiological properties reflecting the integrated canopy processes and characteristics responses to ambient environment. Hence, Penman-Monteith – equation (eq. 6) is an example of a ‘big-leaf’ approach. An alternative to a ‘big-leaf’ model is a two-layer representation of the canopy, where the forest stand is divided to separate over- and understory layers (e.g. Samuelsson et al, 2006). Both frameworks are also appropriate for analyzing EC-measurements if made at two heights (Paper II, IV and VI).

6.4 Forest floor contribution on energy and carbon fluxes

Pine forests in boreal zone have typically a well-developed, extensive overstory layer and a shallow understory layer beneath it, as does the stand at Hyytiälä –site (Figure 12). In Paper V the canopy scale fluxes of carbon and water vapor were modeled using a layer-resolving model and results indicated that both photosynthesis and transpiration rates and the effect of stomatal regulation are significantly different in shaded lower canopy and understory than at the upper canopy. The contribution of forest floor to stand level energy and CO$_2$ fluxes were studied in Papers II and VI while Paper III concentrated on measuring carbon and water
exchange at the forest floor using chamber and EC methods. According these studies, the forest floor (understory and soil) is well coupled to the atmosphere and contributes significantly to forest scale carbon, energy and aerosol particle exchange.

On annual scale the forest floor evapotranspiration varied from 56 to 76 mm, which is between 18 and 25% of the whole-forest values (Paper VI). These fractions are typical for boreal coniferous stands although significantly larger values have been reported in sparser forests (Baldocchi and Vogel, 1996; Baldocchi et al., 1997; Kellidi et al., 1998; Constantin et al., 1999). The forest floor contribution peaks in spring and decreases slightly towards the autumn but seems to remain remarkably constant over wide range of conditions including an intense drought period (Paper VI, Figure 9). In years when snow melts early, as it did in 2007, the forest floor contribution can reach 0.4 – 0.5 immediately after snowmelt, presumably because the early snowmelt allows surface evaporation from the wet soil and mosses but slow recovery of photosynthetic capacity and water and solute transport in the pines hinders transpiration. The typical diurnal cycle of forest floor LE in summer (Paper II, Figure 6) is rather symmetrical with respect to noon and at maximum, forest floor LE reaches 80 – 100 W m\(^{-2}\) and sensible heat flux 100 – 130 W m\(^{-2}\) (Papers II and VI). The sensible heat flux in trunk-space is around 10 to 20% of ecosystem scale \(H\) during the growing season and the contribution is largest in spring. During the snowmelt period in spring the temperature at the snow covered forest floor remains constant (0 °C) while the absorbed radiation heats the canopy leading to strong upward \(H\) above the canopy and downward (between -30 and -20 Wm\(^{-2}\)) in trunk-space providing additional energy for snowmelt. During nights and in wintertime the sensible heat transport from the forest floor is close to zero, primarily because the turbulent exchange above the ground is weak (Papers I and II).

The understory vegetation and soil beneath it are also significant for forest carbon balance. The soil respiration exceeds understory photosynthetic production and the forest floor is a net source of carbon year-round (Papers II and III; Kolari et al. 2009). The strength of the source, however, varies depending on the magnitude of the sub-processes. Understory CO\(_2\) uptake ranges from 1 to 3 \(\mu\)molm\(^{-2}\)s\(^{-1}\) (Papers II and III), which is a similar number than found in other boreal coniferous forests (Baldocchi and Vogel, 1996; Constantin et al., 1999; Law et al., 1999; Subke and Tenhunen, 2004). Annually the forest floor GPP is estimated to be around 100 g C m\(^{-2}\)a\(^{-1}\), about 10% of stand GPP (Kolari et al, 2006), similar contribution than predicted by the multi-layer model for June – July (Paper V). In more open stands this fraction is likely to be significantly larger; a synthesis study of two-layer EC measurements indicated that the understory contribution can reach ~35% in a semi-arid Ponderosa pine forest and ~39% in a deciduous oak forest (Misson et al., 2007). The annual GPP value (~100 g C m\(^{-2}\)a\(^{-1}\)) is small compared to soil respiration (around 600 g C m\(^{-2}\)a\(^{-1}\)), which accounts for ~65% of annual TER (Kolari et al., 2009). In respect to above-canopy EC measurements and knowledge on the magnitude of CO\(_2\) sources and sinks (Kolari et al., 2009; Suni et al., 2003a,c; Paper V), the annual forest floor NEE of 320 g C m\(^{-2}\)a\(^{-1}\) reported in Paper II is likely to be an underestimate and a value closer to 500 g C m\(^{-2}\)a\(^{-1}\) would be more appropriate.
6.5 Seasonal and inter-annual variability

The climate in the boreal zone is characterized by strong seasonal variation with cold, dark winters and rather warm irradiation-rich summers. Accordingly, the energy fluxes between the forest and the atmosphere have strong annual cycle (Figure 13; Paper V). Besides the seasonality of environmental conditions, partitioning of $R_n$ is also strongly modulated by seasonal cycle of vegetation photosynthetic capacity. In March-April, the radiation intensity is already high but photosynthetic capacity still low because of slowness of dormancy recovery (Mäkelä et al., 2004; Arneth et al. 2006; Hari and Kulmala, 2008). Consequently, the photosynthetic demand for atmospheric CO$_2$ is exiguous and the water uptake and transport may be restricted and therefore the trees tend to keep their stomata relatively closed. Because of low transpiration rates, large fraction of available energy is partitioned into sensible heat (Paper VI, Figures 3 – 7) and Bowen ratio ($\beta = H/LE$) peaks (3 – 6) in spring. Over the summer, transpiration increases along the recovering photosynthetic capacity and $\beta$ reaches annual minimum (0.7 – 0.9) in July. Thus, largely caused by seasonal changes in physiology, $H$ peaks in May – June, about two months before LE (Figure 13; Paper V).

The sensitivity of ‘big-leaf’ stomatal conductance to ambient $D$ was studied in Paper V using the model of Oren et al. (1999): $g_s = g_{sref} - m \times \ln(D)$. The sensitivity ($m$) remained rather constant over the whole season but ‘aperture of the stomata’ at $D = 1$ kPa ($g_{sref}$) had a minimum in early spring, increased gradually and exceeded the spring values two – three fold in July – August (Paper VI, Figure 8). Also during drought $m$ remains stable while the $g_{sref}$ decreases strongly (Figure 5; Paper VI). The drought effects become evident at canopy-scale whenever the volumetric water content drops below ~0.15 m$^3$ m$^{-3}$ (Duursma et al., 2008; Papers V and VI). Reduced transpiration causes large fraction of energy to be consumed as sensible heat changing the forest into ‘spring phase’ in terms of energy exchange. Strong and long-term droughts are rare in Finland; during the twelve years studied in Paper VI, drought stress longer than a few days was observed only in summer 1999 and 2006. According to the climate simulations, wintertime precipitation is projected to increase in Scandinavia by 20 – 30 % while the summers are likely to become slightly drier (IPCC, 2007). Thus, the hydrological components of a forest may be altered in the changing climate leading to stronger spring drainage. Long-term droughts, however, are not expected to increase in Northern Europe; in contrary to Mediterranean region (IPCC, 2007). Annual evapotranspiration was rather constant and showed no trends in 1997 – 2008. On average it was 327 mm, roughly half of the precipitation, and varied less than 15 % around the mean. This is because years with high evaporative demand (high radiation and $D$) are characterized by stricter stomatal control and hence lower $g_s$ (Paper VI, Figure 10) and the evapotranspiration rates remain less variable than would be assumed based on the variability of meteorological conditions. Consequently, any change of incoming radiation primarily affects the sensible heat exchange (Paper VI, Figure 10). The invariability of annual evapotranspiration seems typical for boreal coniferous forests (Gielen et al., 2010; Grünwald and Bernhofer, 2007; Tchebakova et al., 2002; Amiro et al., 2006). According to recent
studies evapotranspiration is also quite insensitive to thinning operations (Knoche, 2005; Misson et al., 2005; Vesala et al., 2005; Dore et al., 2010).

The importance of various environmental parameters for controlling eco-physiological processes changes over the year. The recovery of photosynthetic machinery has been attributed to a delayed effect of rising temperatures (Pelkonen and Hari, 1980; Bergh et al., 1998) and consequently GPP (and transpiration) correlates best with air temperature in spring (Figure 14; Suni et al., 2003a,b). Later in the growing season the importance of temperature
decreases and stand GPP becomes primarily dependent on radiation intensity. In contrary to spring, radiation is the main determinant of photosynthetic production in autumn (Figure 14; Suni et al., 2003a,b; Kolari et al., 2007). The environmental factors are naturally also correlated, which complicates analysis of causal relationships. For example, the relationship between daily radiation and temperature depends strongly on the season: In summer the clear skies (high radiation) lead to larger than average daily temperatures while during the winter and autumn the clear days are typically cold and the warm spells are associated with westerlies from the North Atlantic, which typically lead to cloudy and moist conditions in Southern Finland (Figure 14).

Figure 14: Average seasonal cycle of correlation coefficient between gross-primary production (GPP), total ecosystem respiration (TER) and their main environmental drivers, air and soil temperature ($T_a$, $T_s$) and photosynthetically active radiation (PAR). From Paper VII.

The net carbon emissions from northern ecosystems are projected to rise in response to autumn warming and the increased respiration can offset 90 % of the increased CO$_2$ uptake caused by rising spring temperature (Piao et al. 2008). In the wake of Piao et al. (2008) synthesis study considering the whole northern hemisphere, we analyzed the effects of temperature and radiation on autumn carbon balance and its components in detail at Hyytiälä using long-term EC data and a stand photosynthesis model (Paper VII). During autumn, defined as Sept – Dec period in that particular study, radiation intensities diminish rapidly and GPP decreases much faster compared to TER and consequently the forest turns from a carbon sink to a source. In Hyytiälä this has happened on average at 11$^{th}$ of October (range 29$^{th}$ of Sept – 22$^{nd}$ Oct). In Paper VII we found a strong positive relationship between mean air temperature and cumulative NEE both in early (Sept – Oct) and late (Nov – Dec) autumn.
while the sensitivity of GPP to temperature was only marginal (Figure 15). Also model analysis, in which the autumn temperature was stepwise increased while other environmental parameters (radiation, RH) were kept constant, indicated that autumn GPP is rather insensitive to $T$ over projected range of autumn temperatures. The modeled temperature sensitivities were slightly larger than measured ones (Paper VII, Figure 5) but still significantly smaller than found temperature sensitivities for TER. The latter was almost 10 g C m$^{-2}$ °C$^{-1}$ in Sept – Oct and about 4 g C m$^{-2}$ °C$^{-1}$ in Nov-Dec period. In Paper VII the temperature sensitivities of the cumulative GPP and TER were also calculated by a dynamic global vegetation model (ORCHIDEE, Krinner et al., 2005). The model predictions were similar to observed when the $\frac{1}{2}$ h time-step was used but results using daily forcing were, however, biased towards too high temperature dependence of GPP and hence to too low temperature dependence of NEE. The observed bias is presumably because of non-linear relationships between the biogeochemical processes, photosynthesis in particular, and the environmental factors, and highlights the importance of high-resolution forcing data in current models predicting the future carbon cycle.

From the apparent temperature responses found in Paper VII one could conclude that in a boreal coniferous forest TER will increase more than GPP, and the net carbon sink will be reduced if autumn temperatures rise (Figure 15). In autumn and wintertime the warmest periods are typically associated with high cloudiness and large precipitation, conditions favorable for high decomposition rates. The net ecosystem respiration is, however, not only determined by environmental conditions but also by the availability of photosynthates and demand for energy in the plant tissues (Gifford, 2003). The proportion of autotrophic respiration to GPP should stay fairly stable when integrated over long periods of time and is hence constrained by GPP (e.g. Dewar et al., 1998). Waring et al. (1998) suggested that net primary productivity, and correspondingly respiration, would be a constant ratio of GPP. Also a recent FLUXNET-synthesis over wide range of vegetation types showed a tight positive relationship between annual GPP and TER: the year-to-year differences in assimilation explained about 60% of the inter-annual variability of respiration (Baldocchi, 2008). As a large part of heterotrophic respiration originates in rapid utilization of recently produced photosynthates (root exudates) (Pumpanen et al. 2008), also long term (several years) TER should be roughly proportional to GPP. This means that in a warming climate the temporal distribution of the decomposition may change within a year but not necessarily the total cumulative decomposition if the slowly decomposing carbon pools are not affected.
41

Figure 15: Early (Sept – Oct) and late (Nov – Dec) autumn cumulative net ecosystem exchange (NEE) and gross-primary productivity (GPP) regressed against mean air temperature ($T_a$) for respective period. The observed increase of NEE is due to enhanced ecosystem respiration (TER) since GPP is rather insensitive over observed temperature range (Paper VII).

7 Overview of the papers

Paper I considers turbulence, the main transport phenomenon in ecosystem – atmosphere mass, heat and momentum exchange. We studied vertical flow structure using sonic anemometers within and above a quite uniform Scots pine forest for three weeks in summer 2005. We collected mean and higher-order turbulence statistics and ensemble averaged the results to four stability classes to assess the stability effects on canopy flow. Our results resembled other studies made in natural and artificial canopies showing the importance of coherent structures. We found that the diabatic stability above the forest explain large part of the modulations of velocity statistics in CSL except in very stable conditions and immediately above the ground. The results of Paper I were directly used in Paper IV to interpret the particle flux measurements and in Paper V to model the flow regime.
**Paper II** reports turbulent energy and CO$_2$ fluxes measured below the canopy by EC for a full year. We showed that EC can be used in sub-canopy provided the turbulent mixing is adequate and these measurements can be used to estimate the contribution of forest floor to stand CO$_2$ and energy exchange.

**Paper III** quantifies forest floor CO$_2$ and H$_2$O exchange rates by chamber and EC methods. In addition, the chamber measurements were upscaled to provide an estimate for average photosynthesis rate of forest floor vegetation. We found that understory evapotranspiration and NEE varied significantly depending on the vegetation type enclosed in the chamber.

**Paper IV** considers partitioning of aerosol dry deposition between the canopy crown and forest floor. We measured dry deposition velocities of ultrafine ($d_p$ 10-40 $\mu$m) particles above and in trunk-space of a Scots pine forest by EC for two weeks. We showed that the particle transport between the atmosphere and a forest was controlled by same semi-organized turbulent motions, the sweep-ejection cycle, than exchange of other scalars and momentum. We found that between 10 and 35% of deposition takes place to forest floor, a fraction that decreased with increasing turbulence. The study also validated the EC method to measure particle fluxes within a relative open forest.

**Paper V** links the main canopy processes related to carbon and water vapor exchange to microclimatic variability. We coupled a layer-resolving photosynthesis – transpiration model to a simple radiation scheme and included a turbulent transport model to upscale the CO$_2$ and H$_2$O fluxes from a leaf to canopy. We parameterized the leaf-scale model using needle and shoot gas-exchange measurements and the transport scheme using data reported in **Paper I** and considered the role of stomatal regulation on canopy scale fluxes. The model results were assessed against canopy-scale flux and concentration profile measurements.

**Paper VI** is about energy partitioning in a boreal pine forest. I analyzed twelve years (1997 – 2008) of above-canopy EC measurements along the meteorological data to determine both the typical seasonal characteristics and variability of energy partitioning. The study focused on the ‘big-leaf’ surface conductance and discussed the main causes of the seasonal and inter-annual variability.

**Paper VII** is a case-study and answers to the following question: What is the effect of temperature on autumn NEE and to its components (GPP, TER)? This question was answered using long-term EC measurements combined with modeling approaches.
8 Critical opinion and future use of data

The present study covers rather broad range of processes and phenomena, which fit below the main theme, ‘canopy processes, fluxes and microclimate’. There are both rewards and downsides on the broadness of my thesis. First and foremost, working with variety of measurements and large number of interesting research topics gives space for holistic understanding of the nature and interactions among its different processes. On the other hand, it does not allow one to enter deeply into specifics of some particular phenomenon. This balancing between details and generality, specifics and wide range of subjects, is hence an inherent result of the working process during the last few years. Although the results published in the research papers themselves have undergone the peer-reviewing process, I feel obliged to critically comment some of them and briefly consider few potential future research questions that could be assessed based on the results and data provided in this thesis.

In my opinion the largest deficiency of the present work, beyond the broadness, is the uncertainty analysis of the turbulent fluxes – which is primitive as its best. Although this applies for majority of ecosystem – atmosphere studies published nowadays, it should not be taken as a status quo but instead as a challenge with immense practical importance. The primitive uncertainty analysis done in the present work is not by negligence or unawareness but rather because there are no straightforward ways or ready tools to explicitly account the several uncertainty sources related to instrumentation, footprint issues and gap-filling. Hence, to do the uncertainty analysis cleanly would require extensive research and merit separate studies. Despite of this, the systematic measurement errors and uncertainties of seasonal and annual balances (Papers II, VI and VII) should have been analyzed in more detail.

Random errors in EC measurements are related to several sources including instrumental noise, random variability of turbulent transport and spatial and temporal variability of source-sink distribution (footprint characteristics) (Hollinger and Richardson, 2005). By definition, the magnitude of random error decreases when sample size increases and hence random uncertainty has lesser importance for annual balances compared to systematic uncertainty. The systematic errors in EC flux estimates occur as a result of many uncertainty sources such as instrument response time, path-averaging and physical separation of sensors. In addition, selective errors can occur by exclusion of high- and low-frequency flux contribution. The above systematic errors are, however, taken account using various correction procedures (Aubinet et al., 2000; Massman and Clement, 2004). Other possible sources of systematic uncertainty, such as advection, are more difficult to quantify and may lead to large uncertainties in annual balances. On annual scale the propagating systematic uncertainty is large compared to NEE. Rannik et al. (2006) studied two above-canopy EC setups separated horizontally by about 30 m distance at SMEAR II and suggest that uncertainty of annual NEE is about 80 g C m$^{-2}$ a$^{-1}$ (or ~30 %). They eliminated the errors related to flux calculation procedure and concluded that the propagating uncertainty arises mainly from daytime observations and is likely to be linked more to variation of flow field over complex terrain than to heterogeneity of the forest structure and processes. Their annual uncertainty estimate
resembles other studies, which report errors order of 50 – 130 g C m\(^{-2}\) a\(^{-1}\) or 13 – 54 % of NEE (Baldocchi et al., 2003; Oren et al., 2006; Loescher et al, 2004). Hence, there is large uncertainty in the annual balances derived from EC measurements, which needs to be recognized.

**Paper I** is one of the first research papers considering explicitly how diabatic stability affects statistical properties of canopy turbulence. The results themselves can be used to calibrate within-canopy turbulent transport models required in layer-resolving SVAT-schemes\(^8\) and to provide evaluation data for theoretical considerations. This was also the primary motivation of the particular study. It may also serve as a “first-order guide” for interpreting the potential conditions when EC measurements may not represent the desired net ecosystem exchange, in SMEAR II in particular. The main shortcoming of the dataset presented in **Paper I** is the lack of detailed within-canopy temperature profile, which could give more insight on the actual stability conditions within the canopy and close the ground. There are also several topics not touched in **Paper I**. For instance, the synchronized dataset could be re-analyzed to explore spatial correlations of vertically separated measurements to provide detailed information on progression and length-scales of intermittent coherent structures. In addition, the vertical variability of co-spectra should be carefully analyzed, both from a theoretical point of view and to provide necessary model to correct the sub-canopy EC measurements for high-frequency attenuation. The latter problem was not solved but rather circumvented in **Papers II** and **IV**, which is the main shortcoming of those particular studies.

In my opinion, **Paper V** is pivotal for this thesis since it combines the turbulent transport (**Paper I**), biological processes taking place at each canopy element or compartment (**Papers II** and **III**) and variations in canopy microenvironment and upscales leaf-scale processes to canopy scale. It also highlights the uncertainties associated with upscaling from leaf to canopy, information highly valuable when modeling canopy photosynthesis and transpiration. **Papers II, IV, VI and VII** rely primarily on EC measurements of mass and energy exchange and are based on the assumption of horizontally homogeneous source area around the measurement mast. The effects of horizontal inhomogeneities, always present in natural sites, are difficult to quantify but analyzing the data in ensemble sense as done in this work should minimize the influence of varying source area. **Papers II, IV and VI** considered the partitioning of carbon and water fluxes and aerosol particle dry deposition between the main pine canopy and the forest floor. Therefore, we assumed that the footprint characteristics of sub- and above-canopy EC measurements are similar although the source areas do not fully merge. In addition, we neglected the effect of high-frequency attenuation of sub-canopy fluxes and therefore it is likely that the reported contribution of forest floor to whole-forest fluxes is an underestimate of a few percentage-units. Unpublished results propose that energy balance closure varies with respect to wind direction at SMEAR II, which suggests that either the vegetation and surface characteristics (i.e. source area) of flow field vary systematically.

\(^8\) Surface – Vegetation – Atmosphere Transfer -models
around the measurement tower. The rapid advance of laser-based forest inventory techniques during the last decade may provide detailed and quantitative spatial information on canopy structure, which could be used in three-dimensional canopy turbulence models (e.g. Sogachev et al. 2002; Sogachev et al. 2004) to examine the footprint and flow characteristics and their spatial variability. This may provide insights to better account the systematic uncertainty sources and lead to more accurate annual balance estimates and canopy-level process understanding – prerequisite for European long-term greenhouse gas monitoring program (ICOS)\(^9\).

I hope the multi-level eddy-covariance data accompanied with the meteorological and ecological measurements presented in this thesis (Papers II, IV and VI) could be in the future integrated for testing and developing ecosystem – atmosphere transfer models in their description of physical and biological processes. To succeed in this, one has to consider the data needs, temporal and spatial resolution requirements and accommodate the modeling aims better already when designing the measurements and representing the results. For instance, validation of a canopy hydrology model or a two-layer SVAT –scheme would, besides the measurements already existing at SMEAR II, benefit from representative measurements of surface temperature and net radiation above the forest floor. In addition, intense monitoring of snowpack characteristics such as thickness, temperature profile and water equivalent would be necessary to model the winter conditions. Including the latter could also help to explain the seasonal variability of energy balance closure (Paper VI, Figure 1).

9 Conclusions

This study explored forest – atmosphere interactions in a rather broad sense. It considered the main processes and phenomena governing the turbulent exchange of CO₂, water vapor, heat and aerosol particles. The study used long-term measurements of ecosystem – atmosphere exchange conducted at SMEAR II – research station in Hyytiälä, Southern Finland. Although the scope was limited to a single Scots pine stand, the results are likely to be applicable in other boreal coniferous ecosystems.

The main conclusions of this work, framed to answer the specific questions provided in Section 2 are as follows:

- As expected, the turbulent flow inside the relatively open pine forest showed characteristic features of canopy flows. The fingerprint of sweep – ejection cycle is evident in turbulence statistics and large eddies, ranging from tens to hundred meters in size, are responsible for major part of turbulent transport. The diabatic states in the layer above the canopy explain much of the modulations of the key velocity statistics inside the canopy except in very stable conditions and close the ground. The turbulent kinetic energy in the trunk-space is large due to a large longitudinal velocity variance but it is inactive and contributes little to momentum fluxes. Above the forest floor a logarithmic mean velocity profile is formed and vertical eddies are strongly suppressed modifying power spectra of wind components.

- The eddy-covariance (EC) method proved to be successful for measuring forest floor energy and mass exchange given the turbulent mixing in sub-canopy was adequate as typically during daytime and windy nights. In very stable conditions, however, sub-canopy EC measurements do not represent the net exchange between the forest floor and the atmosphere limiting the applicability of EC to monitor seasonal or annual carbon balance. On annual basis the understory and soil contribute between 18 and 25 % of whole-forest evapotranspiration and between 10 and 20 % of sensible heat exchange. The contribution to stand-level photosynthesis is around 10 % (Kolari et al., 2006).

- Between 10 and 35 % of dry deposition of aerosol particles within size range 10 – 30 nm occurs to understory and soil. To my knowledge, Paper IV was the first to explicitly quantify the importance of forest floor as a deposition surface for ultrafine aerosol particles.

- The vertical variations in photosynthetic rate and transpiration within the canopy are primarily caused by attenuation of light. Assuming that each needle operates its stomata autonomously but that the sensitivity of stomata to microenvironment remains the same throughout the canopy, leads into decreasing water use efficiency
in lower canopy. In other words, assimilation rates decrease more rapidly with height than stomatal conductance, and in lower canopy the influence of $g_s$ on photosynthesis becomes negligible compared to light limitation. Different description of stomatal regulation at shoot-scale can have about 15% impact on upscaled canopy CO$_2$ and 30% influence on H$_2$O fluxes, not a small number considering climate models and variety of hydrological applications.

- Climatic factors have a clear seasonal influence on most surface fluxes, primarily because of the shortwave radiation input from the sun. Besides the seasonal constraints, partitioning of available energy to sensible and latent heat depends on the physiological state of the vegetation. In spring when the trees and their photosynthetic machinery are recovering from dormancy, the stomatal conductance and transpiration remain low. Consequently, sensible heat flux peaks in May – June, about two months before latent heat flux. In late summer longer-term drought stress can lead to a significant decrease of conductance and Bowen ratios may return to the spring level, 4 – 6, compared to normal late summer range of 0.8 – 0.9. Because of stomatal regulation, annual evapotranspiration remains rather stable over range of environmental conditions. Thus, any increase in accumulated radiation affects more the sensible than latent heat exchange. Moreover, the seasonal variability of energy partitioning is much stronger than inter-annual.

- In autumn the low light level obscure the positive effect of increasing temperature on photosynthesis. Therefore, increasing autumn temperature affects the photosynthetic production only marginally while the ecosystem respiration increases significantly. Hence, increasing temperature and lengthening of autumn will presumably lead into larger CO$_2$ emissions to the atmosphere. We could, however, not project whether this will in long-term reduce the annual carbon sink of boreal coniferous forests or only shift the temporal distribution of respiration within a year.
References


Katul G.G., Grönholm T., Launiainen S. and Vesala T. 2010c. The effects of the canopy medium on dry deposition velocities of aerosol particles in the canopy sub-layer above forested ecosystems. Atm. Env. (accepted)


