DOCTORAL THESIS

Carbon Dioxide and Water Vapour Exchange within a Norway Spruce Canopy

Lasse Tarvainen

Department of Biological and Environmental Sciences,
Faculty of Science, University of Gothenburg

Göteborg, Sweden, 2012

UNIVERSITY OF GOTHENBURG
BIOLOGICAL & ENVIRONMENTAL SCIENCES

Abstract

Terrestrial ecosystems can act both as sinks and sources in the global carbon cycle. Forests are an important part of this system and a good understanding of their carbon balance is essential for assessments of the future climate and for evaluating mitigation strategies.

Much progress has been made in understanding the main processes controlling plant-atmosphere gas exchange and their responses to environmental factors. However, most previous studies that describe the gas exchange have either been based on laboratory experiments or on short field campaigns with measurements representing a limited range of environmental conditions or positions within the canopy. The results may therefore be ecologically unrepresentative. This limits our ability to accurately represent the true interactions between the gas fluxes and their biological and meteorological regulators on a long-term basis.

This thesis addresses the questions regarding spatial and temporal variety of gas exchange in a forest canopy. It is based on carbon dioxide (CO_2) and water vapour (H_2O) exchange measurements carried out between 2007 and 2010 at Skogaryd research site, a 60 year old Norway spruce (*Picea abies* (L.) Karst.) dominated mixed stand growing on drained peat soil in south-western Sweden. The measurements were conducted once every half-hour at several heights in the canopy on three adjacent trees using continuously measuring automated chambers under naturally occurring meteorological conditions. In addition, the concept of optimality of resource allocation within the canopy, with respect to maximising the canopy productivity, was investigated in two modelling based studies.

Strong seasonality and vertical gradients were observed in the shoot-scale gas exchange rates. However, the relative strengths of the vertical gradients were nearly constant over the year. Therefore, no strong seasonal patterns were observed in the vertical variation of resource use efficiencies. This finding supports the use of simple resource use efficiency based models in ecological modelling. Nitrogen is often found to be a key constraint with respect to canopy assimilation in the northern forests. However, it was found that at this nitrogen rich former fen, neither the within-canopy nitrogen allocation pattern, nor the total availability of nitrogen had large effects on carbon assimilation on shoot-scale. Using optimality modelling on the stand-scale it was shown that by constraining the minimum structural

allocation to the lower canopy shoots it was possible to accurately predict the observed properties of the studied stand from easily obtainable meteorological and stand properties.

Stem gas exchange also exhibited strong spatial variation, and was observed to be considerably higher in the upper part of the stem during the main growing period. Ignoring this vertical variation was shown to result in considerable underestimations of the annual stem-scale gas exchange. Despite the fact that the trees at the site were accumulating large amounts of carbon, the studied stand was not a strong carbon sink on the ecosystem scale, owing to the high carbon emission from the soil. It can be concluded from the findings of this study that variation in resource use efficiency and resource availability within a forest stand is of great importance for the CO_2 and H_2O exchanges with the atmosphere.

Sammanfattning

De landbaserade ekosystemen kan fungera både som källor och som sänkor i kolets globala kretslopp. Skogarna är en viktig del av detta system och en bättre förståelse av deras funktion är grundläggande för att kunna skapa noggranna prognoser för det framtida klimatet samt för att kunna forma strategier för att motverka klimatförändringen.

Stora framsteg har gjorts för att bättre förstå de viktigaste processerna som kontrollerar utbytet av koldioxid (CO_2) och vattenånga (H_2O) mellan växter och atmosfär. Många studier baseras dock på antingen laboratorieexperiment eller korta fältkampanjer som representerar en begränsad variation i omgivningsvariabler eller positioner inom t.ex. ett skogbestånd. Detta begränsar våra möjligheter att på ett korrekt sätt beskriva samverkan mellan gasflöden och deras biologiska och meteorologiska faktorer på lång sikt.

För att öka kunskapen om hur utbytet av CO_2 och H_2O mellan ett skogsbestånd och atmosfären varierar över året, och hur utbytet av dessa gaser varierar vertikalt (från toppen till botten) i ett träd genomfördes mätningar av dessa gaser i ett 60-årigt bestånd av gran, *Picea abies* (L.) Karst., vid Skogaryds försöksområde. Mätningarna gjordes mellan 2007 och 2010 då gasutbytet från skotten och stammarna registrerades kontinuerligt på flera olika positioner inom beståndet. Dessutom studerades frågor om optimal resursallokering inom trädens kronor i perspektivet av att maximera produktiviteten i två modelleringsstudier.

Resultaten från dessa studier visar stark säsongsvariation i gasutbytet och i effektiviteten att utnyttja resurserna ljus, vatten och näring. Framförallt är det ljustillgång och temperatur tillsammans med variationen i kapaciteten för fotosyntes, respiration och transpiration som styr säsongsvariationen. Resurseffektiviteten varierar också vertikalt inom beståndet vilket styrs framförallt av den vertikala fördelningen av ljus och näring. Den relativa förändringen inom kronan var dock konstant över året vilket ger stöd för användning av enkla modeller baserade på resurseffektivitet för att beskriva ett skogsbestånds gasutbyte.

I studier av hur resurserna allokerades inom det undersökta beståndet framkom att även om kväve ofta anses vara begränsande för produktivitet i de nordliga skogarna skulle en ökning av kväveinnehållet i det aktuella beståndet ha liten effekt på fotosyntesen. Varken fördelningen av kvävet inom kronan eller den totala

kvävemängden visade sig vara av stor vikt för kolupptaget på barrnivå i det studerade beståndet. Genom användande av optimalitetsmodellering på beståndsnivå visade det sig att minsta möjliga barrstruktur i den nedre delen av kronan hade stor betydelse för fördelningen av egenskaperna hos barren i hela kronan, t.ex. fördelning av kväve och fotosynteshastighet.

Även koldioxdflöden från stammen visade tydlig säsongsvariation och betydligt mer koldioxid emitterades från de övre delarna av stammarna under den period då stamdiametertillväxt ägde rum. Resultaten från denna undersökning visar att om man inte tar hänsyn till den vertikala variationen i stammarnas gasutbyte kan kolflöden från ett träd underskattas kraftigt. När hela ekosystemet studerades visade resultaten att skogen, som växer på mark med högt organiskt, innehåll inte är någon betydande kolsänka på grund av de höga koldioxidflödena från marken. Resultaten utvunna från dessa studier visar att den vertikala variationen i gasutbytet mellan träden och atmosfären är en viktig faktor för hela ekosystemets kolbudget.

List of Papers

The thesis is based on the following papers, referred to in the text by their Roman numbers.

I. Tarvainen L., Räntfors M. and Wallin G. Seasonal and within-canopy variation in shoot-scale resource use efficiency in a Norway spruce stand. *Manuscript*

II. Tarvainen L., Wallin G., Räntfors M. and Uddling J. Weak canopy gradients of photosynthetic capacity and stomatal responsiveness in a fertile Norway spruce stand. *Submitted to Oecologia.*

III. Dewar R.C., Tarvainen L., Parker K., Wallin G. and McMurtrie R.E. Why does leaf nitrogen decline within tree canopies less rapidly than light? An explanation from optimization subject to a lower bound on leaf mass per area. *Accepted by Tree Physiology.*

IV. Tarvainen L., Räntfors M. and Wallin G. Vertical gradients and seasonal variation in stem CO_2 and H_2O efflux within a Norway spruce stand. *Manuscript*

V. Meyer A., Tarvainen L., Nousratpour A., Björk, R.G., Ernfors M., Lindroth A., Räntfors M., Rütting T., Wallin G., Weslien P. and Klemedtsson L. No large greenhouse gas sink in a fertile afforested peatland. *Manuscript*

Abbreviations

A	Photosynthesis
A_n	Net CO_2 assimilation or net photosynthetic rate (μmol CO_2 m^{-2} s^{-1})
AQY	Apparent quantum yield (μmol CO_2 mol photons^{-1})
A_{sat}	Light-saturated net photosynthestic rate (μmol CO_2 m^{-2} s^{-1})
BA	Basal area (m^2 ha^{-1})
C	Carbon
CH_4	Methane
C_i	Intercellular CO_2 concentration (μmol mol^{-1})
CO_2	Carbon dioxide
C_s	CO_2 concentration beneath the bark (μmol mol^{-1})
E	Leaf transpiration (mmol H_2O m^{-2} s^{-1})
E_c	Stem CO_2 efflux (μmol CO_2 m^{-2} s^{-1})
g_b	Bark conductivity to H_2O (mmol H_2O m^{-2} s^{-1})
g_s	Stomatal conductance to water (mmol H_2O m^{-2} s^{-1})
H_2O	Water
J_{max}	Maximum rate of electron transport
LAI	Leaf area index (m^2 leaf m^{-2} ground)
LMA	Leaf mass per area (kg leaf m^{-2} leaf)
LUE	Light use efficiency
N	Nitrogen
N_2O	Nitrous oxide
N_a	Nitrogen per leaf area (g N m^{-2} leaf)
NEE	Net ecosystem exchange (t C ha^{-1} yr^{-1})
N_m	Nitrogen per leaf dry mass (mg N g^{-1} leaf)
NUE	Nitrogen use efficiency
Q_{10}	Change in reaction rate in response to 10 °C change in T
R_d	Leaf dark respiration rate (μmol CO_2 m^{-2} s^{-1})
RUE	Resource use efficiency
SC	Shoot cuvette
T	Temperature
T_a	Air temperature (°C)
T_s	Stem temperature (°C)
V_{cmax}	Maximum rate of ribulose bisphosphate saturated carboxylation
VPD	Vapour pressure deficit (kPa)
W	Stem H_2O efflux (mmol H_2O m^{-2} s^{-1})
WUE	Water use efficiency

Contents

Introduction

Role of forests in climate regulation and climate change

Forests play a key role in regulating the global climate through their effects on the carbon (C) cycle (Bonan 2008; Pan et al. 2011). They have been estimated to store about 45 % of the terrestrial C and contribute 50 % of the terrestrial net primary productivity (Bonan 2008). Pan et al. (2011) estimated recently that forests sequester around 4 Pg C yr^{-1}, or 60 % of the combined emissions from fossil fuel burning and cement production. However, because of the large-scale deforestation occurring in the tropics the net global forest C sink is considerably less than the sequestration and is currently estimated to be in the region of 1 Pg C yr^{-1} and to be located almost entirely in temperate and boreal forests (Houghton et al. 2005; Pan et al. 2011). In addition to their impact on the annual C sequestration, boreal forest ecosystems are known to store large quantities of C (Bonan 2008; Pan et al. 2011). The soil C store has been estimated to constitute 60 % of the total C storage in boreal forests, while only 20 % of the C is found in living biomass and the remaining 20 % is divided between deadwood and litter (Pan et al. 2011). Furthermore, forest ecosystems contribute to climate change mitigation as sources of renewable energy and building materials (Plomion et al. 2001; Canadell and Raupach 2008). They are also the source of several key products in the global economy, such as timber and pulp, which makes a sound understanding of forest growth important also from an economic perspective (Plomion et al. 2001).

On the ecosystem scale C assimilation by forests is mainly through photosynthesis in the foliage of trees. Trees release carbon dioxide (CO_2) from their leaves, stems and roots in response to oxidation of photosynthate needed to meet the energy requirements associated with growth and maintenance costs (e.g. protein turnover, maintenance of ion gradients). This, so called, autotrophic respiration has been estimated to consume a significant fraction of the energy captured by the trees through photosynthesis (Ryan et al. 1997; Maier 2001). Moreover, decomposition of organic matter in the soil leads to a release of CO_2 through heterotrophic respiration and creation of other greenhouse gases, such as methane (CH_4) and nitrous oxide (N_2O). The CO_2 release from the soil by heterotrophic processes can be considerable, especially in the case of soils with high organic content such as peat (Minkkinen et al. 2002). The balance between the assimilation and respiratory release of C together with effects of disturbances, e.g. fires and insect damage, ultimately determines how much of the assimilated C is stored in the long-term and whether an ecosystem is a net C source or sink.

While boreal ecosystems are a significant C sink on the global scale and in the long-term they are also considered highly sensitive to effects of climate change and management (Limpens et al. 2008; DeLuca and Boisvenue 2012). Factors such as soil water status (Silvola et al. 1996; Rapalee et al. 1998), pH (Weslien et al. 2009), fertility (Klemedtsson et al. 2005) and vegetation composition (Minkkinen et al., 2006) are known to influence the C budgets of these ecosystems. Therefore, any changes in these factors, e.g. following drainage, can potentially have large impacts on the ecosystem scale C budgets in the boreal regions. In order to predict future changes in the ecosystem scale C budgets the mechanisms driving the main components of the C cycle must be well understood.

Measuring and modelling ecosystem scale gas exchange

Due to the great number of processes affecting the gas exchange of an ecosystem, measurements have been carried out on various temporal and spatial scales. The three most common approaches for obtaining data for modelling of the ecosystem C and water (H_2O) fluxes are: remote-sensing (e.g. Liu et al. 1997; Ahl et al. 2004; Anselmi et al. 2004), net ecosystem exchange measurements utilising the eddy covariance technique (e.g. Baldocchi et al. 1988; Reichstein et al. 2007), and the use of chamber measurements to investigate the various component fluxes that sum up to the total ecosystem gas exchange (e.g. Wallin et al. 2001; Hall et al. 2009; Ernfors et al. 2011). All three approaches have been extensively utilised and offer differing combinations of spatial integration and degree of understanding of the processes involved. Remote-sensing approaches are able to generate estimates of the gas fluxes on large spatial scales. However, they provide only limited understanding of the mechanisms and relative strengths of the environmental processes contributing to the observed fluxes, and in many cases result only in crude divisions of the observed area to land-use types. The eddy covariance method is used to measure gas fluxes on an ecosystem scale, thereby providing spatially integrated estimates of fluxes that are directly coupled with the specific type of ecosystem studied. The method can, therefore, be used in e.g. assessing the effect of meteorological variables, atmospheric CO_2 concentration and nutrient or water availability on the ecosystem-scale gas exchange. However, eddy covariance studies can only provide indirect information about the relative strengths of the component fluxes, e.g. by estimating ecosystem respiration from night-time data. Furthermore, it is difficult to attribute changes observed in the integrated ecosystem scale flux to any specific process within the ecosystem. The gas exchange of specific parts of the ecosystem can be measured by using specially designed chambers that give detailed information about the process being observed and its response to various environmental drivers. The benefit with using chambers is their

ability to provide mechanistic process understanding that is needed for model improvement and validation. Because the chambers are relatively small modifying their internal climate is straight-forward and allows for determining e.g. leaf photosynthetic capacities under varying temperatures (T) or CO_2 concentrations. An important drawback with chamber measurements is that their results only apply for a specific part of the ecosystem, such as a leaf, a part of a tree stem or a small patch of soil. Therefore, chamber measurements have to be scaled to the ecosystem level in order to assess the larger scale effects of any functional responses detected on the small-scale. In practise, due to patchiness of resource distribution within a forest-stand, this requires using a number simplifying assumptions regarding the spatial and temporal generality of the observed short-term small-scale responses.

While there has been considerable progress in modelling plant and ecosystem scale processes in the past decades much uncertainty still remains. This uncertainty is due to several factors such as limited understanding of the processes involved and the practical limitations on both data collection and model complexity (Knorr and Heimann 2001; Dewar et al 2009; Beer et al. 2010; Weng et al 2011). There are two main approaches to modelling plant responses to environmental drivers. Mechanistic models aim describe the various plant processes and their interactions in great detail, while optimality models aim to maximise a predefined plant process (e.g. growth, canopy net assimilation or C export from the leaves) with respect to constraints on plant traits and environmental factors (Field 1983; Sands 1995; Mäkelä et al 2002; McMurtrie et al 2008; Anten and During 2011; McMurtrie and Dewar 2011). The main advantage of using the optimality approach is that, compared to the mechanistic models, optimality models are relatively easy to parameterise as they utilise simple equations to determine net primary productivity. The drawbacks with optimality models include the need to correctly identify the process to be optimised and the often made simplifying assumption that plant functioning does not change in response to environmental change (Dewar et al 2009; Anten and During 2011).

Regardless of the approach used all models ultimately rely on correct process understanding and presentation of the involved mechanisms. Furthermore, modelling results must be validated against field data to assess model performance and to identify their strengths and weaknesses.

Observed vertical canopy gradients in leaf properties and gas exchange

The long-term average radiation absorption in the canopy declines exponentially with cumulative leaf area (Monsi and Saeki 2005). Therefore, leaves deeper down

in the canopy generally are adapted to more shaded conditions and area-based leaf N content (N_a), leaf mass per unit area (LMA), photosynthetic capacity, dark respiration (R_d) and stomatal conductance (g_s) are known to decrease with light availability and, therefore, depth in the canopy (e.g. Kull 2002; Griffin et al. 2002; Meir et al. 2002; Zha et al. 2002; Han et al. 2003; Han et al. 2004; Sellin and Kupper 2004; Uddling et al. 2009). Moreover, it is often found that the mass based leaf N content (N_m) varies little within the canopy and that N_a and LMA decline in parallel (Ellsworth and Reich 1993; Meir et al. 2002).

The photosynthetic capacity of leaves is strongly dependent on their N content (Field 1983; Evans 1989) owing to the majority of leaf nitrogen being in the Calvin cycle proteins, such as the main photosynthetic enzyme Rubilose-1,5-bisphosphate carboxylase oxygenase (Rubisco), and thylakoid membranes (Evans 1989) that are essential parts of the photosynthetic apparatus. This coupling between light, N allocation and photosynthetic capacity has led to a commonly used assumption in modelling that N distribution and, thus, variation in photosynthetic capacity within the canopy is proportional to absorbed light (e.g. Field 1983; Kull 2002). However, this is not observed in the field as light intensity decreases more rapidly than leaf N content through the canopy (e.g. Hollinger 1996; Lloyd et al. 2010). Several explanations for this discrepancy have been put forward, including varying within-leaf N allocation patterns (e.g. Hikosaka et al. 2005; Terashima et al. 2005) and constraints posed by leaf morphology (Meir et al. 2002) or maximum attainable photosynthetic capacity in upper canopy leaves (Lloyd et al. 2010). However, despite the attention the discrepancy has received over the years there is currently no commonly accepted explanation for it (Lloyd et al. 2010).

In addition to being dependent on the efficiency of the photosynthetic apparatus leaf C assimilation is also strongly affected by CO_2 availability. This availability is controlled by stomata that act to balance the photosynthetic requirements against the inevitable water loss associated with CO_2 uptake. g_s has been observed to be more responsive to light in the lower canopy than in the upper canopy in many species including Norway spruce (Sellin 2001; Sellin and Kupper 2004). Vapour pressure deficit (VPD) and T are also known to affect g_s (Ranney and Peet 1994; Fredeen and Sage 1999; Day 2000; Uddling et al. 2004; Mott and Peak 2010; Peak and Mott 2011), but co-vary under field conditions which makes investigating their effects on mature trees difficult. Moreover, there is currently no commonly accepted mechanism to explain the stomatal responses to T and air humidity (Fredeen and Sage 1999; Mott and Peak 2010; Peak and Mott 2011).

Efficiency of resource use by plants

Within the general framework defined by the vertical gradients in leaf properties and photosynthetic capacity, the observed net photosynthesis (A_n) is limited by light, H_2O and/or nutrients, although other factors such as T can be important over seasonal time-scales (Medlyn et al. 2002; Han et al. 2004; Warren and Adams 2004). This limitation may arise from both the availability of a given resource and the efficiency with which it can be acquired by the plant (Binkley et al 2004). Furthermore, photosynthesis at a given time may be co-limited by any combination of these factors rather than by only a single factor. Variation in light and H_2O availabilities over the year leads to a seasonality in the relative importance of the limitation posed by each resource. Therefore, efficient resource use is an important plant trait that is integral in defining the ecological limits within which a particular plant can grow and be competitive (e.g. Funk and Vitousek 2007).

Resource use efficiency (RUE) can be defined on both long-term and short-term basis and is an adaptive trait over the long-term (years) on species and stand scales (Binkley et al 2004) and an acclimative trait over the short-term on the scale of individual leaves (Niinemets and Tenhunen 1997). The long-term estimation of RUE relies on growth estimates, e.g. above-ground net primary productivity or stem growth, related to canopy-scale light interception and water loss expressed on the annual scale and to the total canopy N content or uptake. Estimates of the short-term RUE are commonly based on measurements of instantaneous leaf-scale photosynthetic rate relative to simultaneously measured light interception, g_s or leaf N content. As these measurements are often made under light-saturated conditions they provide a measure of the resource use capacity of a leaf.

While it has been recently shown, for a beech forest, that upscaling water use efficiency (WUE) from leaf-scale to canopy-scale is feasible on a daily time-scale (Linderson et al 2012), coupling RUE observations made at the different scales is problematic. The responses of RUE to resource availability on the scales of leaves and seconds can be quite different from the responses on the scales of plants or stands and years (Binkley et al. 2004). This difference is not unexpected, and it has been pointed out that maximising long-term RUE does not necessary involve continuously maximising short-term RUE (Cowan and Farquhar 1977). It has also been noted that the leaf-scale photosynthesis in evergreen trees, such as Norway spruce, is often limited by inadequate resource availabilities and by sub-optimal T (Warren and Adams 2004). Therefore, the benefits of being capable of achieving high photosynthetic rates, and thus high short-term RUE, under optimal conditions may be of only limited value for these trees (Warren and Adams 2004). In fact,

from an efficiency perspective it would seem reasonable to expect that leaf, plant and stand-scale resource use optimisation would reflect the long-term rather than the short-term RUE.

Stem carbon dioxide efflux

In addition to assimilatory products used in maintaining both leaf area and efficient foliage function, trees must allocate C and photosynthate to the woody-tissue. This is seen as the expansion of branches, stem and roots to allow for growth of new foliage and to ensure that the tree has sufficient access to resources, such as N, H_2O and light, to remain competitive with respect to its neighbours. In addition, photosynthate is required as an energy source for the living cells in the woody biomass. Since photosynthesis occurs mainly in the leaves the distribution of photosynthate from foliage to the other parts of the tree occurs against a water potential gradient and requires energy consuming active transport processes (Jensen et al. 2011). Respiration by the living cells in the woody biomass causes CO_2 to be released within the stem and the roots. The CO_2 release by the roots is commonly studied in the context of soil respiration, and the autotrophic respiration by roots has been found to be highly significant fraction of the ecosystem scale C budget (Ryan et al. 1997). Of the above-ground woody compartments, stems are the more intensively studied owing to their greater economic importance.

The CO_2 release from stems is strongly coupled with T, through its effects on cellular activity, and growth (Ryan et al. 1995; Zha et al 2004; Acosta et al. 2008). Respiration is strongly T dependent and varies over the year, while growth is mostly concentrated to the summer months. The analysis of stem CO_2 efflux (E_c) is further complicated by the fact that CO_2 concentration at a given point along a stem at any given time is affected by several simultaneously occurring processes. These processes include the CO_2 release from woody-tissue respiration, CO_2 transport in the xylem sapflow and within-stem storage of CO_2 (McGuire and Teskey 2004; Bowman et al. 2005). The strength of the xylem transport has been found to vary in response to canopy transpiration with low values commonly observed during the night, but it can significantly affect the E_c during the day (McGuire and Teskey 2004; Bowman et al. 2005). Stored CO_2 has been found to be a relatively constant fraction of the total stem CO_2 when considered over the long-term (McGuire and Teskey 2004). Moreover, several additional factors have been suggested to modify the CO_2 release from stems. For example, variation in stem temperature (Edwards and Hanson 1996; Stockfors 2000), the strength of the diffusion barriers within the stem (Pruyn et al 2002; Teskey and McGuire 2002; Steppe et al. 2007) and the

distribution of living cells in the stem volume (Ryan 1990; Stockfors and Linder 1998a) are known to influence the strength of the observed E_c.

Despite this well known variability in E_c it has only rarely been determined over the entire year and is often measured only during the daytime. Also, while it has been shown that E_c can exhibit considerable spatial variation along the stem (Sprugel 1990; Ceschia et al. 2002; Damesin et al. 2002; Cavaleri et al 2006; Hermle et al. 2010) most studies to date have been conducted at breast height.

Scope

The main objective of this thesis is to understand the within canopy variation in resource allocation and use in a Norway spruce, *Picea abies* (L.) *Karst.*, stand, and connect this variation to patterns in the CO_2 and H_2O exchanges between the trees and the atmosphere. Furthermore, the effects of seasonality on the gas exchange and the within canopy gas exchange gradients are also addressed.

Paper I investigates long-term shoot-scale RUE with respect to its variation within the canopy and over the year.

Paper II addresses the variation of photosynthetic capacity within the canopy and investigates the importance of within-canopy N allocation with respect to maximising canopy photosynthesis using the optimality concept. In addition to this Paper II also studies the vertical variation in stomatal responsiveness to environmental drivers.

Paper III aims to explain the discrepancy between the theoretically optimal and the observed canopy gradients in N_a by utilising optimality modelling. Stand characteristics predicted by the model are compared with field observations made in the Norway spruce stand.

Paper IV describes the vertical and seasonal patterns of stem CO_2 and H_2O effluxes and also addresses the question of whether the vertical variation is connected to variation in bark conductivity to gas between different stem positions. The effect of ignoring the vertical gradients when making annual estimates of stem CO_2 and H_2O effluxes is also investigated.

Paper V assesses the annual ecosystem scale C sink-source status of the Norway spruce stand (Fig. 1) using both the eddy covariance technique and a combination of chamber and biomass measurements.
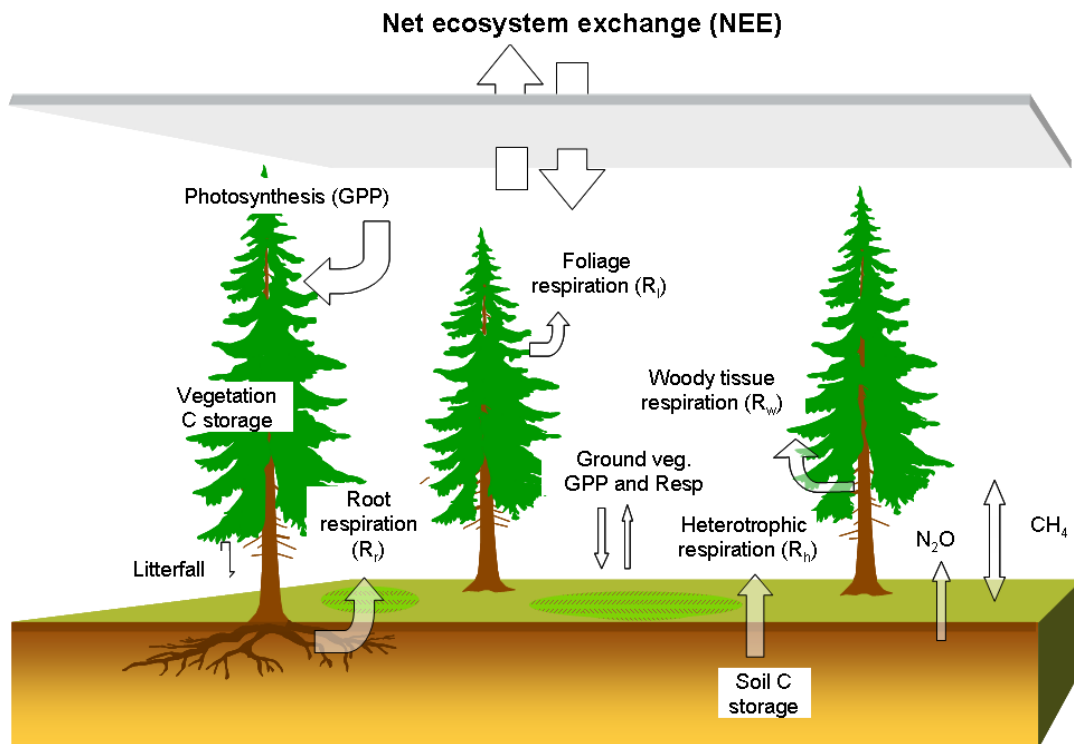
Figure 1 Processes contributing to the net ecosystem exchange at Skogaryd research site.

Material and methods

Experimental setup

The studies included in this thesis were conducted between 2007 and 2010 in a mature mixed coniferous stand in southwest Sweden (Skogaryd research site; 58° 23' N, 12° 09'E; 60 m.a.s.l.). The stand was dominated by Norway spruce, *Picea abies* (L.) Karst. (82% of basal area, BA), but Scots pine, *Pinus sylvestris* L. (13% of BA) and Silver birch, *Betula pendula* Roth (5% of BA), were also present (Fig. 2).

Figure 2 Stand structure at Skogaryd research site. Yellow = Birch, Red = Pine, Green = Spruce, Light Green = trees used in gas exchange measurements.

The dominant and co-dominant Norway spruce trees were 22 - 25 m in height and had breast height diameters (dbh, 1.3 m) of 0.26 – 0.35 m, while the base of the green crown varied between 7 and 11 metres within the stand. In 2010 the stand density was approximately 1000 trees ha^{-1} and the basal area at breast height 45 m^2 ha^{-1}. The leaf area index (LAI) at breast height varied between 5.8 and 6.5, with the lowest values observed immediately prior to bud break in the spring and the highest after the expansion of the new shoots was completed. The study area was a former fen, with a deep (> 1 m) peat layer, that was drained in the 1870s and used for agriculture before the plantation with Norway spruce in 1951. For details on the soil properties and description of the understory vegetation, see Klemedtsson et al. (2010) and Björk et al (2010). The annual mean temperature and precipitation at the meteorological station nearest to the site (Vänersborg, 12 km east of Skogaryd) were 6.2 °C and 709 mm, respectively, during the 1961 – 1990 climatic period. The 2007 - 2010 mean temperature was 6.9 °C and mean precipitation 904 mm (www.smhi.se). The annual variation in above canopy light interception, expressed as photosynthetic photon flux density (PPFD), as well as, air temperature (T_a) and VPD measured in the upper canopy during 2007-2009 are shown in Fig. 3.
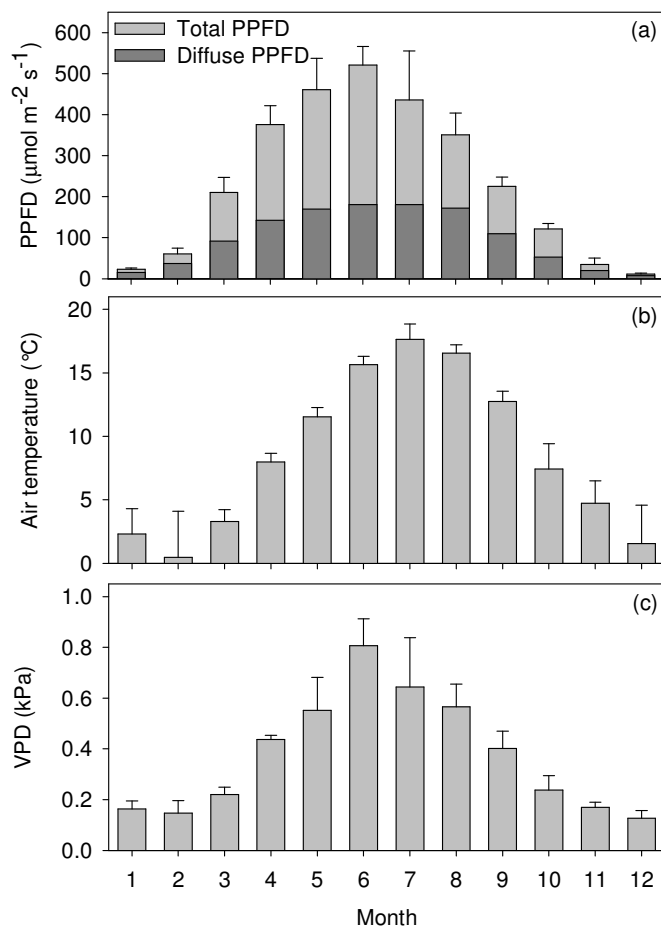

Figure 3 Monthly mean (+ SD) (a) total and diffuse photosynthetic photon flux densities (PPFD), (b) air temperature and (c) vapour pressure deficit (VPD) at the top of the canopy 2007 - 2009

Shoot gas exchange (Papers I – III)

The gas exchange (CO_2 and H_2O) of one-year-old Norway spruce shoots was measured continuously between 2007 and 2009 at five heights (approximately 22 - 24 m, 20 – 22 m, 18 - 20 m, 14 - 16 m and 11 - 12 m above ground, hereafter called levels 1 to 5, Fig. 4) in three dominant trees (with crown base at 11 m) using a custom made multichannel gas exchange system running in an open mode (Wallin et al 2001; Hall et al 2009). Temperature controlled shoot cuvettes (SC) were connected by heated and insulated tubing to infra red gas analysers (CIRAS-1 PP Systems, Hitchin Herts, U. K.) located in a nearby cabin (< 25 m away). Shoot segments (55 mm long) were enclosed in the SCs which were made out of transparent Plexiglas that allowed approximately 90 % of the incoming radiation to reach the shoot inside the cuvette. PPFD was measured adjacent (< 5 cm) to the SCs using a leveled and cosine-corrected quantum sensor (PAR-1(M), PP Systems). Direct and diffuse radiation were measured above the canopy with a sunshine sensor (BF-2, Delta-T Devices Ltd, Cambridge, U.K.) simultaneously to the measurements of PPFD at each SC. Temperatures inside and outside the SCs were monitored and the inside temperatures kept on average 0.2 °C above the ambient to avoid condensation along the cuvette walls. Each of the 15 SCs was measured for 30 seconds once every 30 minutes. The gas exchange system does not allow for separating between photosynthesis and respiration and, therefore, all photosynthesis data reported in this study are presented as net values. The system has been used previously to study the gas exchange of Norway spruce at the Flakaliden research site in northern Sweden (Wallin et al. 2001; Hall et al. 2009).
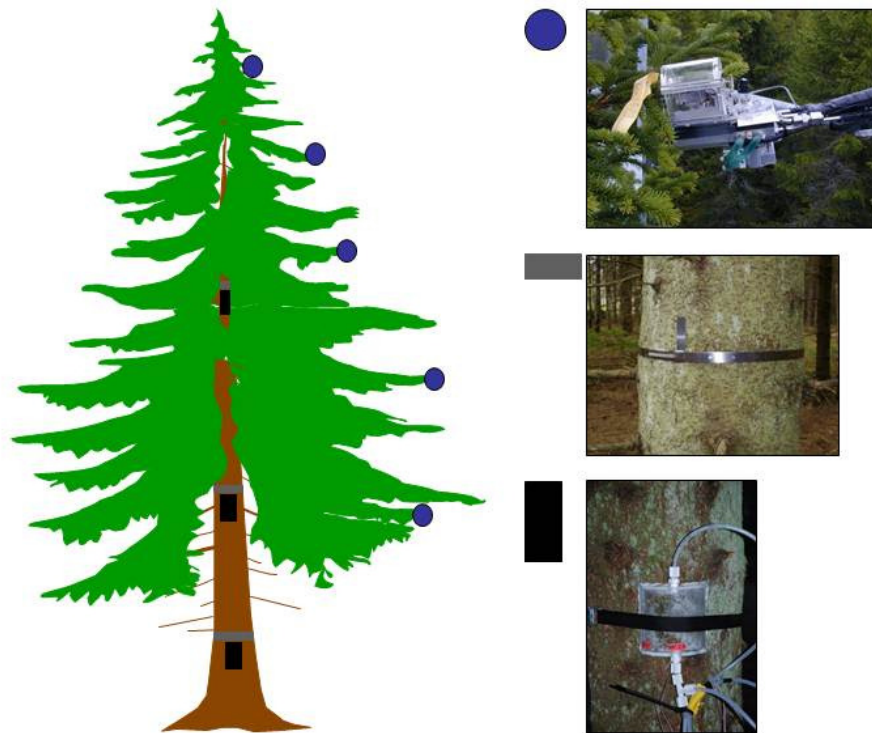
Figure 4 Top - cuvette for measuring shoot gas exchange. Middle - manual dendrometer band for measuring stem increment. Bottom - chamber for measuring stem gas efflux.

Photosynthetic capacity (Paper II)

To determine the within-canopy variation in photosynthetic capacity measurements of the photosynthetic response to intercellular carbon dioxide concentration (C_i), so called A-C_i curves, were conducted at four canopy levels (1, 3 - 5) on each tree in June 2009, September 2009 and June 2010. The A-C_i curves were determined using LI-6400 Portable Photosynthesis System with a conifer chamber (6400-05; Li-Cor Biosciences, Lincoln, NE, U.S.A.) running in energy balance mode. The biochemical model of C_3 photosynthesis described by Farquhar et al. (1980) was used to parameterise the maximum rates of ribulose bisphosphate saturated carboxylation (V_{cmax}) and electron transport (J_{max}) for each measured shoot.

Determination of the physical and chemical properties of the needles (Papers I – III)

The shoots used in the continuous gas exchange measurements were changed approximately every second month while the shoots used in the assessment of within-canopy photosynthetic capacity variation were harvested directly after the measurements were completed. Once a shoot was harvested its spatial properties; one-sided projected shoot, needle and axis areas, as well as, average needle

dimensions and the total number of needles were determined using a flatbed scanner (Epson 1600+ equipped for dual scanning) and WinSEEDLE analysis software (WinSEEDLE Pro 5.1a, Regent Instruments Inc., Canada). The needles and the axes were then dried at 70 °C until constant mass. The dry mass and the projected needle area were used to obtain the LMA. A ball mill (MM 400, Retsch, Düsseldorf, Germany) was used to grind the dry needles into a fine powder that was analysed for its C and N contents using an elemental analyser (EA 1108, Fison Instruments, Italy). The needle N contents together with needle mass and area estimates were used to calculate N_m and N_a, respectively. A more intensive shoot sampling consisting of 15 trees (the three used in this study and 12 others) was carried out in March 2011 and showed that the shoot properties of the three studied trees were representative of the larger sample.

Stem efflux and diameter increment (Paper IV)

E_c and stem H_2O efflux (W) were observed between 2008 and 2010 using 9 additional chambers connected to the automated gas exchange system described above. The stem chambers were constructed from transparent acrylic plastic (Perspex) pipes with diameters of 8 or 10 cm depending on the stem diameter at chamber position. The chambers covered a stem surface area between 99.6 and 104.1 cm^2 and had volumes that varied between 230 and 310 cm^3 (assuming circular stem cross-section). Loose bark was removed prior to fastening the chambers to the stem using adjustable straps. A reusable adhesive (Blu-tack, Bostik) was used as an additional sealant at the chamber-stem interface. The chambers were oriented towards south and aluminium plates installed over them as radiation shielding. The flow rate through the chambers was 750 cm^3 min^{-1}.

Stem effluxes were measured on the same three trees as the shoot-scale gas exchange (**Papers I – III**) at three heights (1.3 m, 10 m and 18 m) corresponding to breast height, crown base and mid-crown (Fig. 4). E_c and W were measured at each position once every 30 minutes over the three year study period. T_a and stem temperature (T_s) at the depth of 5 mm in the stem, measured by copper-constantan thermocouples, were determined at each chamber location simultaneously to the gas efflux measurement. Manual dendrometer bands were installed adjacent to each stem chamber in October 2007 and stem diameters measured manually twice a year (Fig. 4). Furthermore in May 2008 automated dendrometer bands (D6 Strain-gage clip-sensor, UMS, Munich, Germany) that recorded the stem diameter every 30 minutes were installed at the 1.3 m and 10 m levels.

Determination of the stand-scale C budget (Paper V)

Two approaches were used to determine the net ecosystem exchange (NEE, Fig. 1) of the stand. NEE was measured directly using the eddy covariance technique (e.g. Baldocchi et al. 1988; Reichstein et al. 2007) and determined indirectly from a combination of biomass (stem growth, litter fall) and chamber (soil efflux) measurements. For details on the used methodologies refer to **Paper V**.

Results and Discussion

Vertical radiation and needle property gradients in the canopy (Papers I-III)

The patterns of light availability and shoot properties within the canopy were similar to those observed in previous studies (e.g. Ellsworth and Reich 1993; Brooks et al. 1996; Bond et al. 1999; Stenberg et al. 1999; Kull 2002). Light interception decreased exponentially through the canopy (Fig. 5a) and the thickness of the needles varied along the vertical gradient with the LMA of upper canopy shoots being approximately twice that of the lower canopy shoots (Fig. 5b). N_a also approximately doubled between the top and the bottom of the canopy needles (Fig. 5c), while no vertical variation was observed in N_m (Fig. 5d). No significant differences were detected in the needle properties or their vertical variation between the growing (April - September) and non-growing (October - March) seasons.
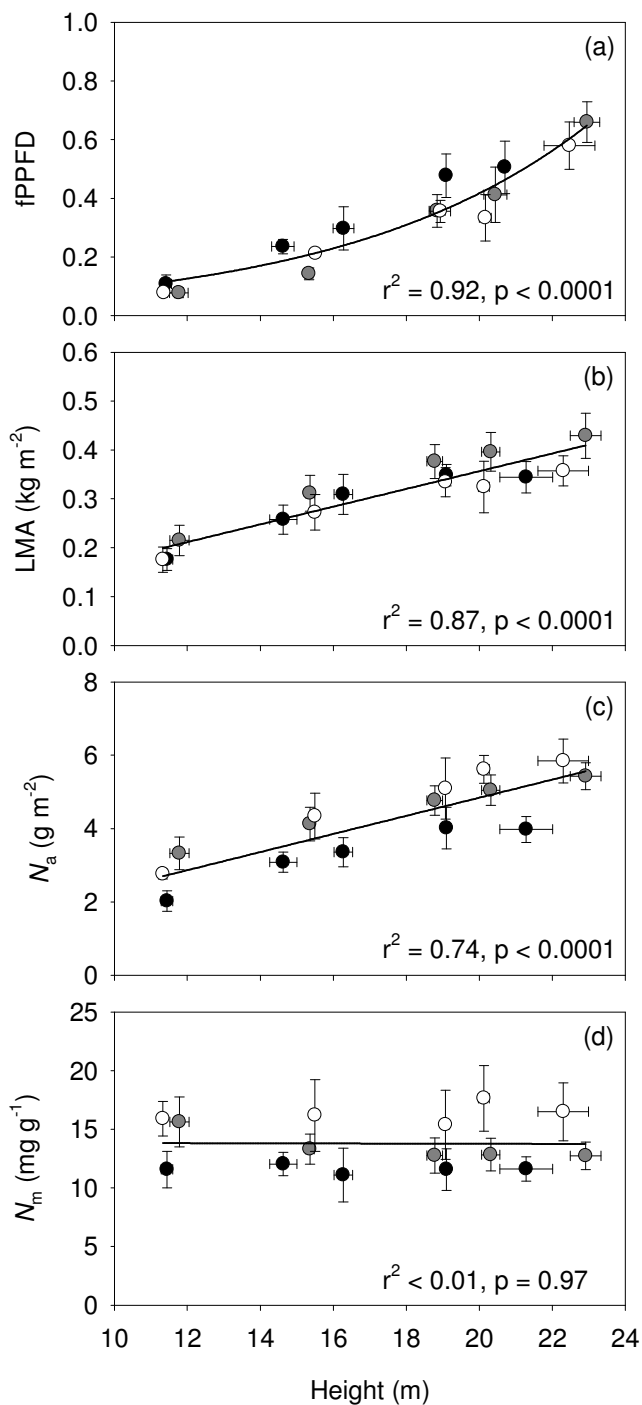
Figure 5 Radiation interception and needle properties in relation to canopy position (means ± s.d.) in April-September 2007-09. (a) Fraction photosynthetic photon flux density (fPPFD), (b) leaf mass per unit area (LMA), (c) area-based needle nitrogen content (N_a) and (d) mass-based needle nitrogen content (N_m).

Seasonality and vertical variation in shoot-scale net gas exchange performance and capacity (Papers I and II)

The monthly mean net CO_2 assimilation (A_n), R_d and transpiration (E) peaked during the summer at all canopy levels (Fig. 6). The relative amplitude of the seasonal variation at the top of the canopy was the higher for A_n than for R_d and E mainly due to the very low photosynthetic activities observed in January and December (Fig. 6a, c and e). The relative strengths of the vertical A_n and R_d gradients did not vary significantly between the two periods with the values observed at the bottom

of the canopy consistently being approximately 20 % of those at the top (Fig. 6a - b and c - d, respectively). There was little vertical variation in the observed E during the summer (Fig. 6f), while a trend towards higher transpiration from the lower canopy shoots was detected during the winter (Fig. 6f). The lower canopy shoots were observed to exhibit stronger stomatal sensitivity to PPFD compared to the upper canopy shoots under similar environmental conditions (Fig. 4c in **Paper II**). This may partly explain the weak dependence of E on canopy position observed during the summer.
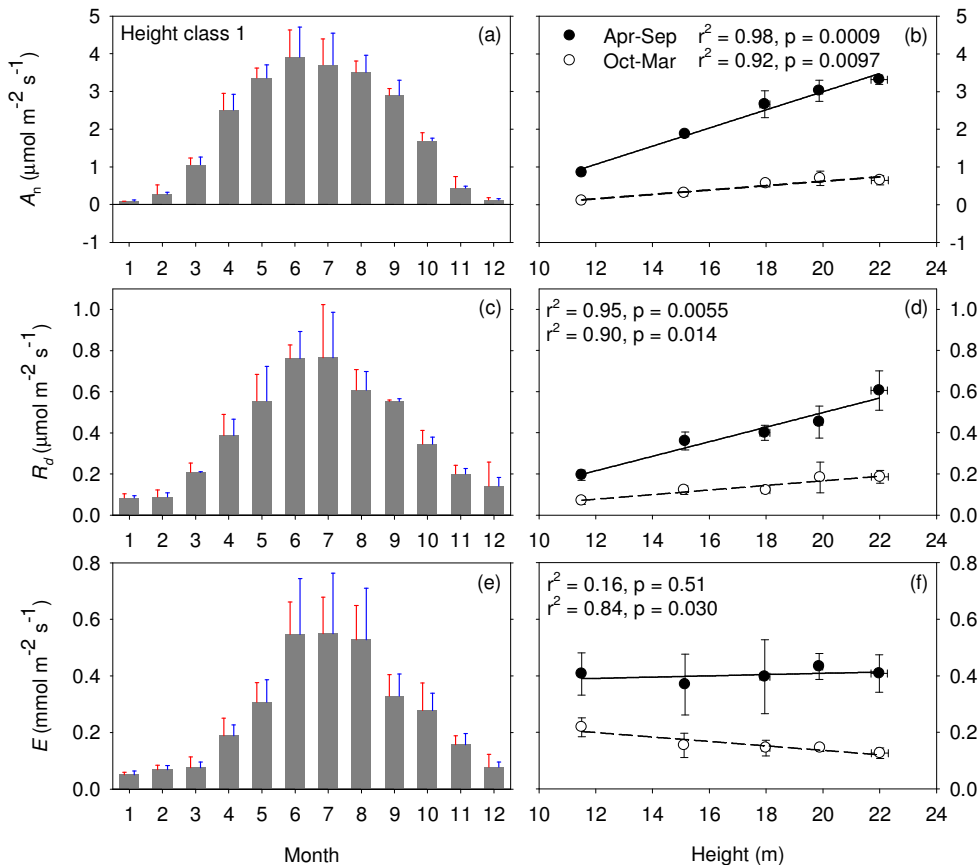
Figure 6 Shoot-scale gas exchange in 2007 - 2009 (mean ± s.d.). (a) Net CO_2 assimilation (A_n) of top of the canopy shoots, (b) vertical variation in A_n, (c) dark respiration (R_d) of top of the canopy shoots, (d) vertical variation in R_d, (e) transpiration (E) of top of the canopy shoots and (f) vertical variation in E.

Similarly to the mean gas exchange rates, clear seasonality was observed in the parameters describing the gas exchange capacities of the shoots (Fig. 7a, c, e and g). Light-saturated photosynthetic rate (A_{sat}), apparent quantum yield (AQY) and g_s peaked during the summer as expected owing to the strong seasonal control of gas exchange exerted by light availability and T. The temperature sensitivity of R_d (Q_{10}) was lowest during the summer, as has been observed before (e.g. Stockfors and Linder 1998b). The observed vertical gradients (Fig. 7b, d, f and h) in April – September were

only significant for A_{sat} and g_s that have been commonly observed to vary along the vertical gradient (e.g. Kull 2002; Griffin Similarly to the mean gas exchange rates, clear seasonality was observed in the parameters describing the gas exchange capacities of the shoots (Fig. 7a, c, e and g). Light-saturated photosynthetic rate (A_{sat}), apparent quantum yield (AQY) and g_s peaked during the et al. 2002; Meir et al. 2002; Zha et al. 2002; Han et al. 2003; Han et al. 2004; Sellin and Kupper 2004; Uddling et al. 2009). The limited light availability and low temperatures during the winter did not allow for determination of vertical capacity gradients during the October – March period.
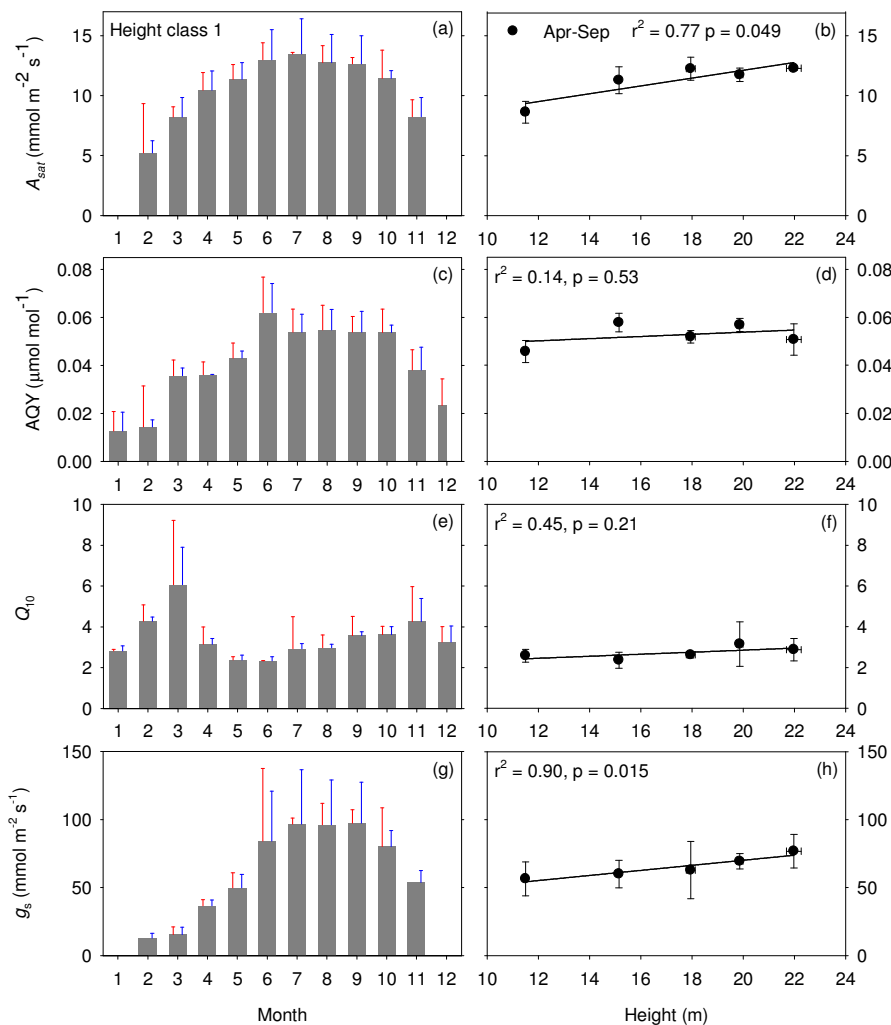
Figure 7 Shoot-scale gas exchange capacity in 2007 - 2009 (mean ± s.d.). (a) Light-saturated net photosynthesis (A_{sat}) in top of the canopy shoots, (b) vertical variation in A_{sat}, (c) apparent quantum yield (AQY) in top of the canopy shoots, (d) vertical variation in AQY, (e) temperature response of shoot respiration (Q_{10}) in top of the canopy shoots, (f) vertical variation in Q_{10}, (g) stomatal conductance (g_s) in top of the canopy shoots and (f) vertical variation in g_s.

The response of shoot photosynthetic capacity to N_a, and therefore to the vertical shoot position, differed between observations made within a month of bud burst in June and in September. V_{cmax} and J_{max} at 25 °C were well related to N_a in September 2009 but not in June 2009 or 2010 (Fig. 8a-b). A possible explanation for this observation is that N is stored as Rubisco prior to bud burst, as observed in a *Pinus pinaster* stand in south-western Australia (Warren and Adams 2001).
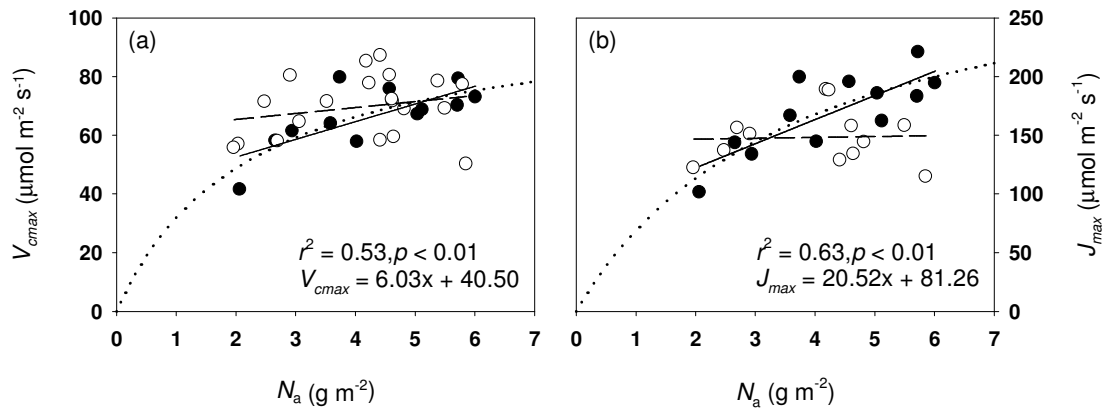

Figure 8 Maximum rate of (a) ribulose bisphosphate saturated carboxylation (V_{cmax}) and (b) electron transport (J_{max}) *vs.* N per unit area (N_a) in September 2009 (filled circles, solid line) and in June 2009 and 2010 (open circles, dashed line). The dotted line shows the asymptotic function used in modelling shoot photosynthesis in **Paper II**. The regression equations and statistics refer to the September data.

Stomatal sensitivity to environmental drivers (Paper III)

No significant vertical gradients were detected in stomatal sensitivity to VPD (Fig. 4b in **Paper II**). However, the light response of g_s was found to be more sensitive in the lower canopy (Fig. 4c in **Paper II**), in accordance to previous findings for Norway spruce (Sellin and Kupper 2004). This allows lower canopy shoots, which exist in an environment with constantly changing light conditions, to use water more efficiently (Sellin and Kupper 2004). The observation that temperature was more strongly related to g_s at low than at high VPD (Fig. 9) contrasts previous findings reporting stronger T responses of g_s at high VPD (Fredeen and Sage 1999; Mott and Peak 2010) and suggests that for the studied shoots the effect of T on g_s was less important than the limitation posed by VPD.
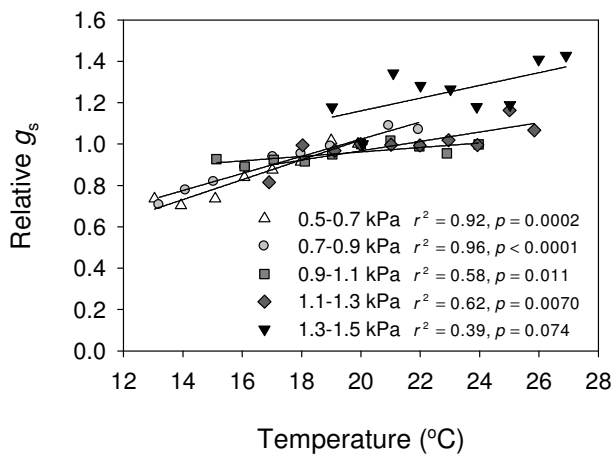
Figure 9 Average light-saturated stomatal conductance (g_s) relative to g_s at 20 °C in the upper canopy (canopy levels 1-3) within different 0.2 kPa intervals of vapour pressure deficit (VPD) *vs.* temperature (*T*).

Optimality of shoot-scale N allocation (Paper II)

Nitrogen allocation between shoots at different canopy levels was found to be close to optimal with respect to maximising photosynthesis (Fig. 10a). However, the resulting total net photosynthesis of the 12 shoots that were included in the modelling study was not found to be very sensitive to N allocation. Allocating N among the studied shoots according to observed, optimal and homogeneous patterns resulted in predicted total C assimilations by the shoots that were within 2 % of each other (Fig 10b). This is considerably less than the simulated 11 % difference between observed and optimal N allocation patterns in *Nothofagus fusca* in a study by Hollinger (1996). Furthermore, for a number of non-woody species optimal N allocation has been found to result in an increase of between 5 % and 14 % in total canopy photosynthesis (Anten 2005 and references therein).
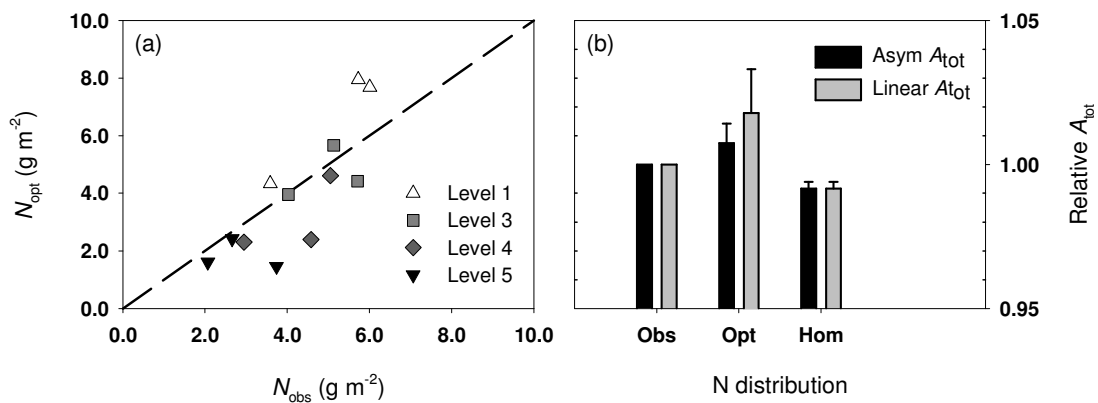

Fig. 10 (a) Optimal within-canopy N allocation (N_{opt}) with respect to maximising integrated shoot net photosynthesis (A_{tot}). *vs.* observed N allocation (N_{obs}) (b) Variation in predicted A_{tot} with N allocation pattern. Obs = observed N allocation; Opt = optimal N allocation predicted by the model; Hom = homogeneous within-canopy N allocation.

Variation in the needle N content was also found to have only a limited effect on the total C assimilation of the studied shoots (Fig. 11a) owing to the observed weak V_{cmax} and J_{max} responses to N (Fig. 8a-b). In fact, the modelling results indicate that increasing the water availability of the shoots, simulated as increased g_s, would have been more beneficial to their total C assimilation than greater N availability (Fig. 11b).
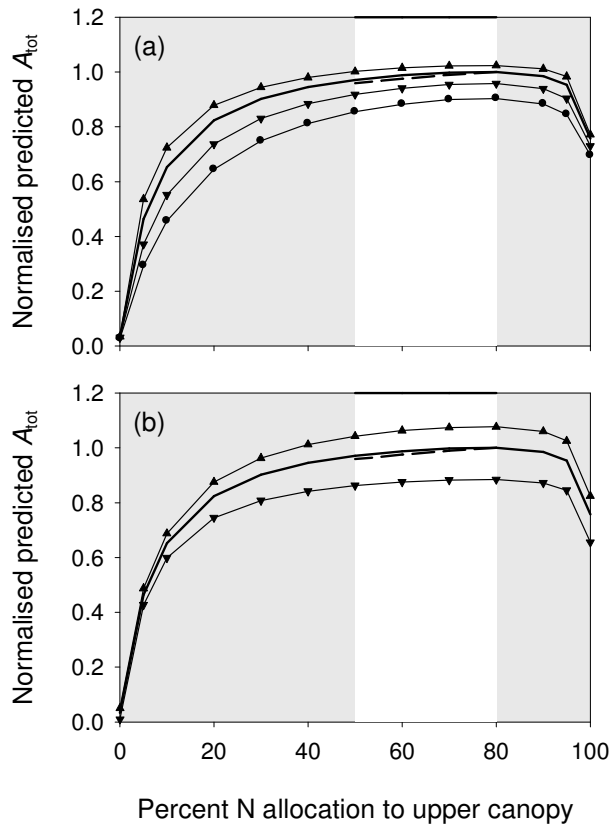

Figure 11 Sensitivity of C assimilation summed for shoots at different canopy heights (A_{tot}) to (a) canopy N distribution and summed shoot N content (N_{tot}) and (b) stomatal conductance (g_s). A_{tot} normalised to 1 at 80 % N allocation to the upper canopy levels (level 1+3 relative level 1+3+4+5). Solid lines = A_{tot} modelled using asymptotic photosynthetic capacity *vs.* N per unit area (N_a) relationship in Fig. 2 (upward triangle +30 % N or g_s, downward triangle – 30 % N or g_s, circle – 50 % N. Dashed line = A_{tot} modelled using linear photosynthetic capacity *vs.* (N_a) relationship.

It has previously been found that a larger amount of N available at the stand scale can increase the photosynthetic capacity of individual leaves in some cases (e.g. Mitchell and Hinkley 1993; Murthy et al. 1996; Kellomäki and Wang 1997), while it has no effect in others (Pereira et al. 1992; Laitinen et al. 2000; Sigurdsson et al. 2002; Elvir et al. 2006; Talhelm et al. 2011). The weak sensitivity of C assimilation to N indicated by the simulations performed in this study may be due to the high fertility of the site (cf. Kellomäki and Wang 1997) or limitations by other nutrients as observed in N-saturated stands in north-eastern United States (Elvir el al. 2006). On the leaf-scale it is known that when N_a is low increasing N has a strong positive effect on photosynthesis, but that this effect becomes weaker as N_a increases (Cao et al. 2007). In cases when no increases in leaf N and photosynthetic capacity are observed in response N addition it is commonly found that the additional N results in production of new leaf area (e.g. Pereira et al. 1992; Sigurdsson et al 2002; Turnbull et al. 2007). However, since the model used in this study only investigated

the effects of altered N content and allocation in a canopy with a fixed structure, any possible changes in total assimilation due to altered leaf area remain unknown.

Shoot-scale resource use efficiency and stand-scale optimality (Papers I - III)

In **Paper I** it was shown that the long-term shoot-scale RUE varied seasonally with each of the efficiencies (light, H_2O and N) peaking at different times of the year (Fig. 12a, c, and e). This suggests that the relative importance of each of these limiting resources varied over the year.
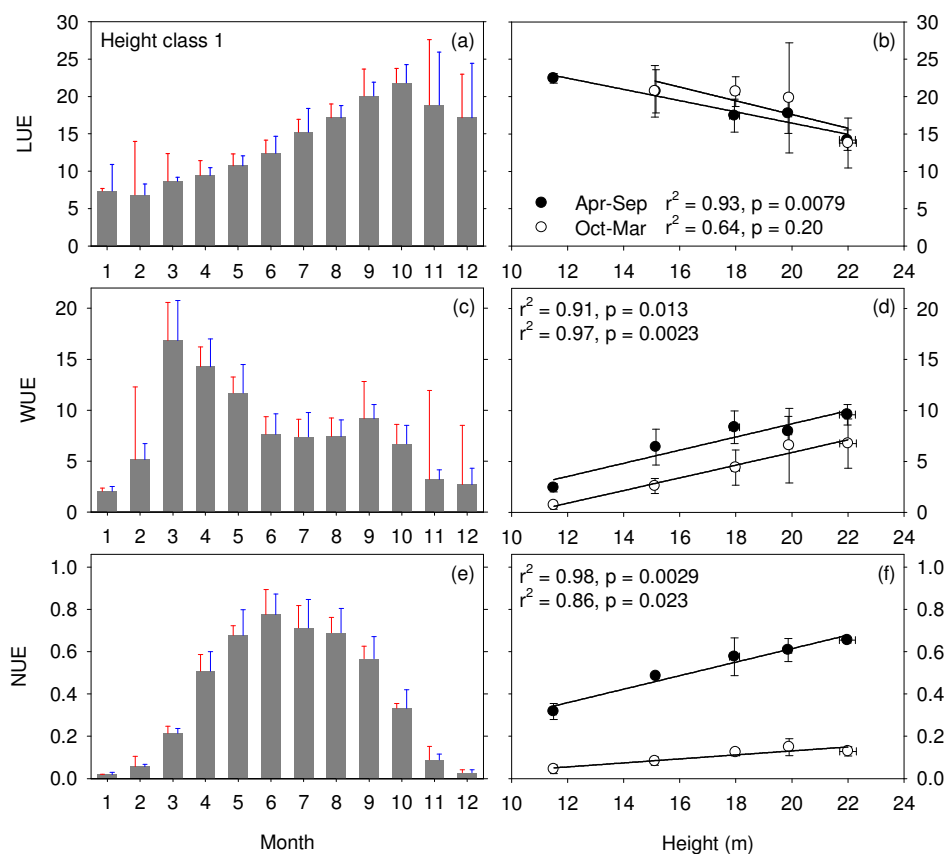

Figure 12 Shoot-scale resource use efficiency in 2007 - 2009 (mean ± s.d.). (a) Monthly light use efficiency (LUE_m) in top of the canopy shoots, (b) vertical variation in LUE_m, (c) monthly water use efficiency (WUE_m) in top of the canopy shoots, (d) vertical variation in WUE_m, (e) monthly water use efficiency (NUE_m) in top of the canopy shoots, (f) vertical variation in NUE_m.

Shoot-scale light use efficiency (LUE) peaked during the autumn because during the summer, when the peak A_n was observed (Fig. 6a) the light availability often exceeds what can be utilised by the photosynthetic apparatus due to substrate limitations. In the autumn A_n was still relatively high (Fig. 6a) while the average light availability was much less than during the summer (Fig. 3a). WUE of the

shoots peaked during the spring due to the photosynthetic system starting to recover while E remained low in response to low soil and air temperatures and the associated low VPD (Figs. 6a and c and 3b-c, respectively). Since N_a did not vary significantly over the year, seasonality in the shoot-scale NUE was mainly due to variation in A_n (Fig. 6a). However, it should be pointed out that this study was not designed to specifically assess the seasonality in needle N. Quite possibly, pooling the data over the seasons may have masked needle N content variation occurring on shorter time-scales. Furthermore, the weak sensitivity of shoot-scale C assimilation to N suggested by the modelling may indicate that seasonal changes in N allocation do not occur to any great extent at this N rich site.

While the absolute RUE values varied between the growing and non-growing seasons the vertical gradients were qualitatively similar during both periods (Figs. 12b, d and f). LUE was lower in the upper canopy due to the shoots experiencing light-saturated conditions more frequently than the lower canopy shoots. As the E did not vary much with canopy position (Fig. 6c), the observed increase in WUE with height reflects the vertical A_n gradient observed during both seasons (Fig. 6b). NUE was observed to be highest in the upper canopy (Fig. 6f). This pattern was due to light interception declining more strongly than N_a with canopy depth (Fig. 5a and c) and, thus, more N was allocated to the lower canopy needles than was required for maximising their C assimilation. This was also suggested by the difference in the observed and predicted optimal N allocation patterns, and the weak effect of altered N availability, on the integrated C assimilation of the studied shoots (**Paper II**, Fig. 10a). A possible reason for N_a in the lower canopy being higher than expected based on optimality theory (Field 1983) was explored in **Paper III**. In this study it was postulated that there is a lower limit to N allocation to the bottom of the canopy shoots that results from structural requirements posed on the needles by exposure to factors such as wind stress and herbivory. It was then shown utilising the optimality concept that by constraining LMA and by implication, since N_m was assumed constant within the canopy in agreement with observations (Fig. 5d), N_a of the lower canopy needles resulted in a predicted within canopy N allocation pattern that agreed well with observations (expressed as k_N in Table 1). In addition to explaining the observed N allocation pattern, the model was successful in predicting several other key canopy traits such as LAI and total canopy N content, based on easily obtainable meteorological and stand property data (Table 1 in **Paper III**).

Table 1. Columns 1-2: summary of key foliage and canopy properties measured in the Norway spruce stand; all data are averages over three trees. Column 3: optimal values predicted by the MAXX optimization hypothesis.

Foliage/canopy property	Measured	Modeled
Key traits used as model parameters		
Canopy light extinction coefficient, k_L (m^2 ground m^{-2} leaf)	0.43	-
Needle mass per unit area in bottom layer[a] (kg DM m^{-2} leaf)	0.181	-
Key traits predicted by MAXX		
Extinction coefficient for leaf N, k_N (m^2 ground m^{-2} leaf)	0.18	0.19
Canopy-average needle N concentration (mg g^{-1})	14.5	14.0
Total canopy N content (g N m^{-2} ground)	21.3	21.6
Other traits		
Total canopy LAI[b] (m^2 leaf m^{-2} ground)	5.1 ± 1.3[c]	5.05
Light-saturated photosynthesis in top layer[d] (μmol CO_2 m^{-2} leaf s^{-1})	12.3 ± 1.9[c]	13.4[e]
Mean needle N content in top layer[d], N_a (g N m^{-2} leaf)	5.18 (6.13[f])	6.70[e]

[a]11-12 m; [b]at 11 m (base of green crown); [c]one standard deviation; [d]22-24 m; [e]value predicted at $L = 0$; [f]maximum value measured within the top layer (22-24 m) of each tree, averaged over the three trees.

Increasing g_s of the studied shoots by 30 % was predicted to result in a 8 % increase in their integrated C assimilation (**Paper II**) thereby suggesting that increasing water availability would have resulted in a lower stand-scale WUE, but higher LUE and NUE over the simulated period. Since shoot-scale light availability was not affected by the simulations in **Paper II**, LUE on both shoot- and stand-scales would have increased with the increased C assimilation following an increase in either N or H_2O availability.

However, as noted above, the modelling study carried out in **Paper II** did not allow for changes in the canopy structure. It is likely that, in accordance to previous findings on the effect of increasing stand-scale resource availability on stand-scale RUE (e.g. Pereira et al. 1992; Fife and Nambiar 1997; Sigurdsson et al 2002; Turnbull et al. 2007), at least some of the increased resource availability would have been utilised in increasing stand-scale RUE through development of additional foliage.

Variation in stem respiration and growth (Paper IV)

In accordance to previous findings from studies carried out in the lower part of the stem (Lavigne and Ryan 1997; Maier 2001; Zha et al. 2004), E_c exhibited strong seasonality (Fig. 13a) that mirrored the seasonality in T_a (Fig. 3b) and T_s (Fig. 1b in **Paper IV**). Furthermore, during the growing season mid-stem E_c was considerably higher than the E_c observed on the lower stem levels, while no E_c gradient was observed during the non-growing season (Fig. 13a). This observed seasonal pattern persisted even when E_c was scaled to common T using the observed T sensitivity of E_c (Q_{10}) (Fig. 3a in **Paper IV**, Fig. 13b), indicating that while important with respect to the efflux through its direct effects on cellular respiration T could not explain all the observed variation in E_c as has been observed before (Stockfors and Linder 1998a; Maier 2001). It is, therefore, likely that much of the observed E_c during the growing season is related to either local release of CO_2 in response to growth, or results from transport from other parts of the plant-soil continuum in the xylem water stream (Levy et al. 1999; McGuire and Teskey 2004).
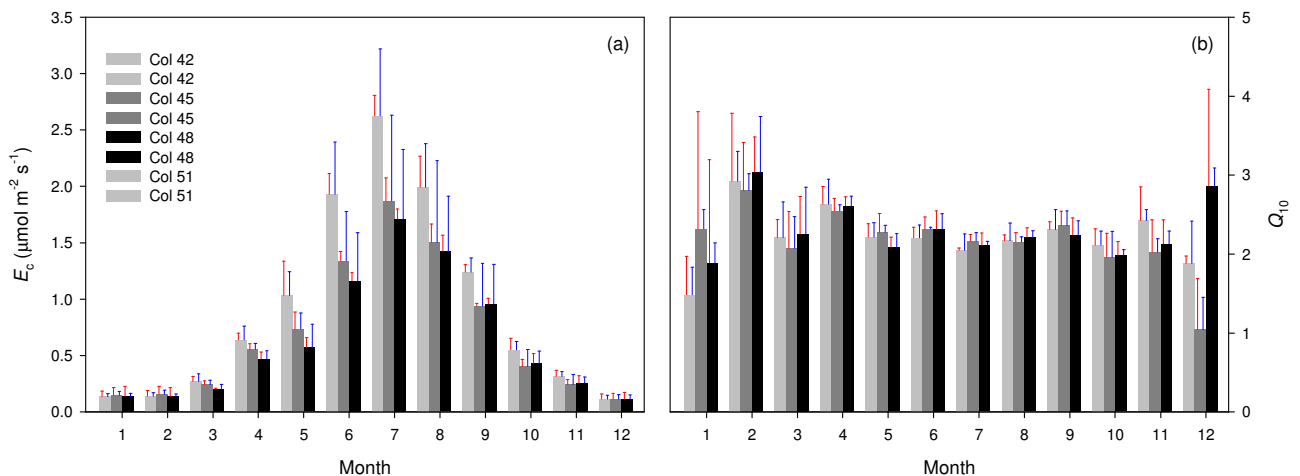

Figure 13 Stem (a) CO_2 efflux (E_c, µmol m-2 s-1), and (b) temperature sensitivity of E_c (Q_{10}, unitless) at three stem heights. Monthly means for 2008 - 2010 are shown ± s.d. of annual (red) and between tree (blue) variations.

W varied in a pattern similar but less distinct than that observed in E_c (Figs. 14a and 13a, respectively). Although bark conductance (g_b) varied over the growing season (Fig. 14b) the pattern was similar at all stem positions and, thus, did not explain the observed vertical variation in E_c (Fig. 13a) or in W (Fig. 14a).
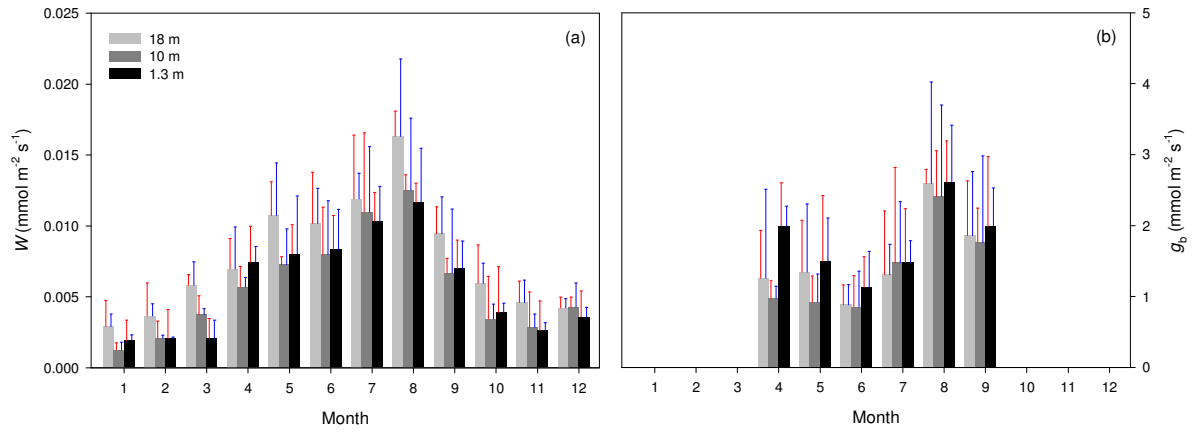
Fig. 14 (a) Stem H_2O efflux (W, mmol m^{-2} s^{-1}), and (b) bark conductance (g_b, mmol H_2O m^{-2} s^{-1}) in April - September. Monthly means for 2008 - 2010 are shown ± s.d. of annual (red) and between tree (blue) variations.

The CO_2 concentration beneath the bark (C_s) was determined using g_b, E_c and the atmospheric CO_2 concentration (Fig. 15). These calculations revealed that in order for the observed E_c patterns to occur C_s at mid-stem would have had to have been 2 - 3 times higher than C_s at the lower stem positions (Fig. 15). The observed monthly mean T_s did not differ greatly between stem positions (Fig. 1b in **Paper IV**) which was also the case for Q_{10} of the E_c (Fig. 13b) which suggests that the higher C_s did not result from stronger warming of the upper stem position. As the large C_s differences were detected during May - July, which corresponds to the main diameter growth period (Fig. 4a-b in **Paper IV**) it is possible that the high C_s calculated for the mid-stem reflects higher relative growth rates at this position compared to the lower stem (Table 1 in **Paper IV**). Furthermore, due to the closer proximity to the foliage, the mid-stem C_s is likely to be influenced more by the processes occurring in the phloem than the lower stem C_s.
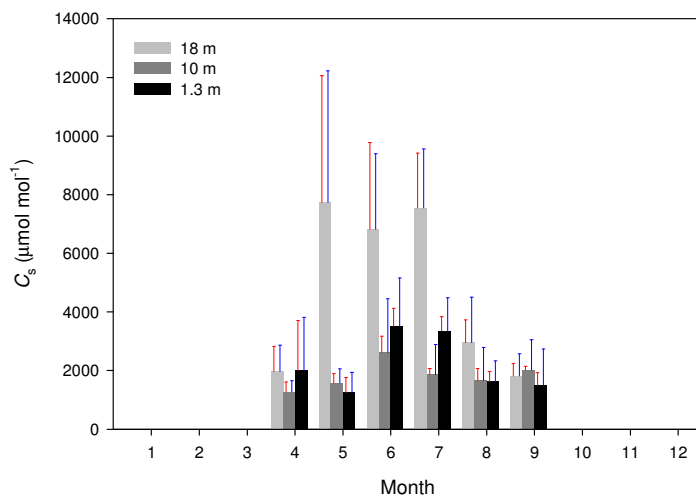

Figure 15 CO_2 concentration (C_s, μmol mol^{-1}) beneath the bark layer in April – September. Monthly means for 2008 - 2010 are shown ± s.d. of annual (red) and between tree (blue) variations.

It has been shown previously that E_c varies spatially (Sprugel 1990; Ceschia et al. 2002; Cavaleri et al. 2006). When E_c at this site was estimated on the scale of the entire stem it was found that ignoring the vertical variation in E_c resulted in, on average, 13 % underestimation of the annual efflux compared to a scaling that included a simple representation of the observed vertical variation in the efflux rates (Table 2). While considerable differences were observed between the trees in the studied stand (Table 2), the results indicate that using efflux rates measured at breast height can lead to considerable errors in estimations of tree-scale autotrophic respiration rates.

Table 2 Annual tree-scale stem CO_2 (*E*) and H_2O (*W*) efflux and the ratio between efflux estimates based on measurements at 1.3 m and on vertical integration. Means are shown ± s.d. of between tree variations. Abbreviations: int = vertically integrated efflux, 1.3m = efflux estimation based on data from 1.3 m level.

Year	E_{int} mol CO_2 m^{-2} stem yr^{-1}	$E_{1.3m}$ mol CO_2 m^{-2} stem yr^{-1}	$E_{1.3}/E_{int}$	W_{int} mol H_2O m^{-2} stem yr^{-1}	$W_{1.3m}$ mol H_2O m^{-2} stem yr^{-1}	$W_{1.3}/W_{int}$
2008	23.5 ± 5.8	21.1 ± 4.6	0.90 ± 0.03	179 ± 34	164 ± 23	0.92 ± 0.06
2009	22.7 ± 6.6	20.0 ± 7.5	0.87 ± 0.07	218 ± 52	201 ± 52	0.92 ± 0.09
2010	21.8 ± 5.3	18.6 ± 7.0	0.83 ± 0.12	188 ± 61	178 ± 69	0.92 ± 0.18

Seeing the forest for the trees (Paper V)

The ecosystem scale C budget at the Skogaryd research site was estimated using two approaches (Figure 16). The eddy covariance technique and the combination of biomass and chamber measurements resulted in different estimates of the C source-sink status of the studied stand (-2.0 t C ha^{-1} a^{-1} and 1.0 t C ha^{-1} a^{-1}, for eddy covariance and the combined methods, respectively), mainly due to the high uncertainty in the chamber measurements of the soil C efflux. However, both estimates of the net flux between the stand and the atmosphere were close to zero suggesting that the stand is near neutral with respect to C. Both methods are subject to large uncertainties and the need for improvement in making estimates of stand scale C cycling is highlighted by the differing results between the two methodologies used here. It is, however, evident that while trees grow well at this fertile site, the mitigation potential presented by the large C uptake in the woody biomass is largely compensated for by the considerable amounts of C and N_2O released from the soil due to decomposition of soil organic matter (Table 4 in **Paper V**, Fig. 16). Moreover, as the stand ages, tree growth will slow down and, thus, assimilation of C into the woody biomass will be less effective in

compensating for the high soil C efflux. Furthermore, the effect of the expected future temperature increase is likely to stimulate soil CO_2 release considerably more than tree growth. Therefore, it can be concluded from the findings in **Paper V** that afforestation is not a suitable long-term mitigation option with respect to fertile former peatlands that have been drained and converted to agricultural use.
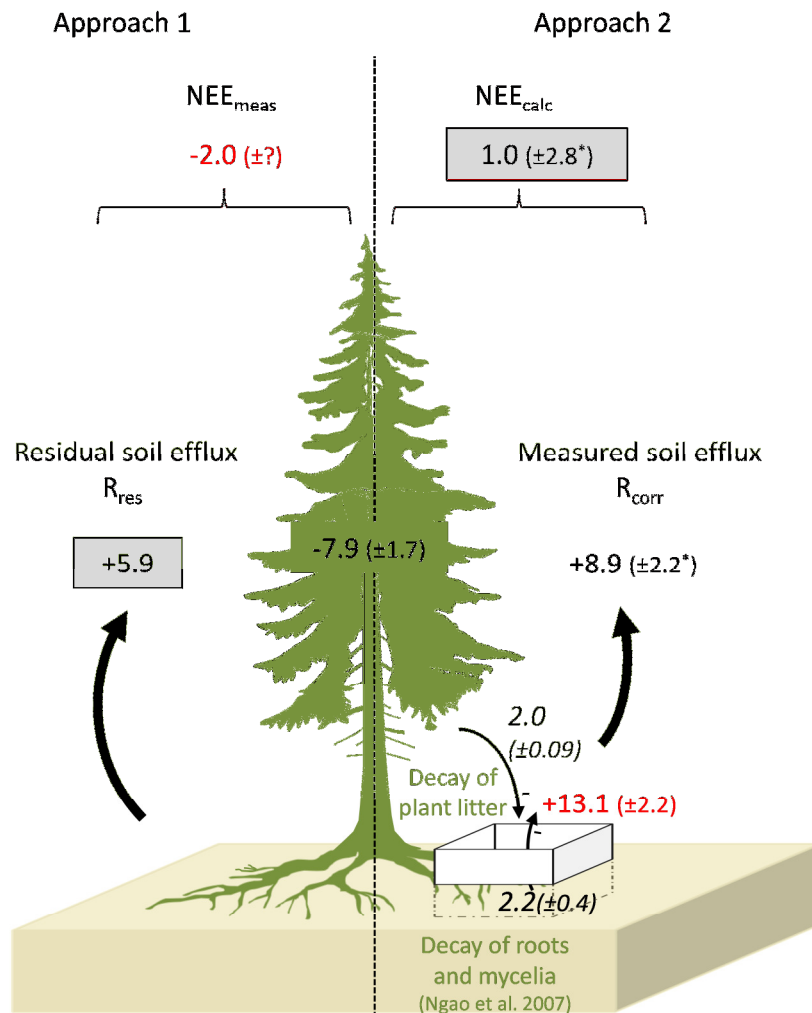

Figure 16 Net ecosystem exchange (NEE) at the Skogaryd Research site as determined by two approaches. In approach 1 (left), the residual soil efflux R_{res} is determined based on the measured NEE_{meas} and the calculated tree growth. In approach 2 (right), the NEE is determined as the residual flux NEE_{res} based on the measured soil efflux R_{meas} and the calculated net fluxes from root/mycelia decay and decomposed plant litter. Measured gross fluxes are given as red numbers, calculated gross fluxes as black numbers, calculated net effluxes as italics. Fluxes determined as residuals are given in grey boxes. Values are given in t C ha^{-1} a^{-1}.

* standard errors were calculated according to the Gaussian error propagation scheme

Key Findings

In **Paper I** it was found that despite the strong seasonality and vertical gradients observed in the shoot-scale gas exchange rates, the relative strength of the vertical variation did not change over the year. Therefore, no strong seasonal patterns were observed in the vertical variation of resource use efficiencies.

The main finding of **Paper II** was that at a N-rich site neither the within-canopy N allocation pattern nor the total availability of N had large effects on the C assimilation by the shoots. Optimal N allocation in the studied shoots was predicted to result in a less than 2 % increase in the integrated C assimilation, whereas altering the total N in the shoots by 30 % was predicted to result in a 2 – 4 % change in the C assimilation.

In **Paper III** it was shown that the observed vertical canopy N allocation pattern could be predicted within the optimality modelling framework by constraining the minimum structural allocation to the lower canopy shoots. The canopy properties predicted by using this approach were found to be in a close agreement with observations.

Paper IV examined the vertical variation of stem CO_2 and H_2O effluxes. It was shown that using the common assumption of effluxes along the stem being proportional to the efflux at breast height resulted in a 13 % underestimation of the annual tree-scale CO_2 efflux, while the annual tree-scale H_2O efflux was underestimated by 8 %. It is suggested that the observed vertical pattern in the CO_2 efflux during the growing season is due to higher growth rates and stronger influence by phloem processes in the upper stem.

In **Paper V** it was found that the studied fertile Norway spruce stand was neither a strong source nor a strong sink of C. With the C accumulation to woody biomass likely to decrease with stand age it was concluded that afforestation is not a suitable strategy with respect to mitigating greenhouse gas emissions from agricultural soils with high organic content.

Concluding Remarks

The results presented in this thesis indicate that while defining leaf capacity under controlled conditions, such as light-saturation, is certainly useful in both understanding tree function and in modelling, it is also necessary to investigate seasonality and within-canopy variation of CO_2 and H_2O exchanges under naturally occurring conditions. This allows for coupling the capacity estimates to actual gas exchange rates that are strongly influenced by within-canopy resource distribution patterns and their seasonal variation. As expected, owing to the general annual patterns of light availability and temperature, seasonality was observed to be a major factor with respect to all the gas fluxes investigated in this thesis. It is, however, notable that while the absolute rates of shoot-scale net gas exchange and the resulting resource use efficiencies vary strongly along the vertical canopy gradient at any given time their relative strengths appear invariable between the seasons. This observation provides support for modelling approaches that use simple canopy-scale resource use estimates to scale observations to larger spatial scales. However, one should keep in mind that resource distributions and acquisition efficiencies are subject to change in response to changes in the environmental drivers and that the observed proportional relationships may not be valid under future conditions. CO_2 release from stems was observed to vary strongly over the year and, in contrast to shoot-scale observations, to exhibit a distinct seasonal pattern in its vertical variation in response to variation in growth rates between stem positions. While long-term observations of the stem CO_2 efflux gradients are rare, it is clear from the result presented in this thesis that ignoring these gradients when estimating stand scale C release may cause considerable errors.

On the scale of individual shoots it was found that at this N-rich site the actual within-canopy N allocation pattern and stand-scale N availability did not significantly affect the integrated C assimilation of shoots located at several canopy positions. However, as the simulation was carried out assuming fixed canopy structure any possible changes in canopy-scale C assimilation in response to altered leaf area following changes in N were not accounted for, although they certainly might be significant.

The optimality modelling approach was found to be remarkably accurate in estimating the properties of the studied Norway spruce stand. Assuming that lower canopy needles were required to have a certain amount of structure to be able to withstand the effects of mechanical stresses and herbivory resulted in a predicted

optimal N allocation pattern close to that observed in the canopy, thereby providing a potential explanation for the well-known discrepancy between within-canopy light and N distribution patterns. This finding should, however, be further tested with data from other stands to investigate its general validity.

Thus, it is concluded that vertical patterns in resource use efficiency and resource availability are of great importance for a complete understanding of the CO_2 and H_2O exchanges between trees and the atmosphere. The large contribution of the C uptake by woody biomass observed in the ecosystem-scale C budget clearly indicates that a better understanding of tree growth and responses to environmental change is a key concern with respect to climate change mitigation.

References

Acosta M, Pavelka M, Pokorny R, Janous D, Marek MV (2008) Seasonal variation in CO2 efflux of stems and branches of Norway spruce trees. Annals of Botany 101:469-477

Ahl DE, Gower ST, Mackay DS, Burrows SN, Norman JM, Diak GR (2004) Heterogeneity of light use efficiency in a northern Wisconsin forest: implications for modeling net primary production with remote sensing. Remote Sensing of Environment 93:168-178

Anselmi S, Chiesi M, Giannini M, Manes F, Maselli F (2004) Estimation of Mediterranean forest transpiration and photosynthesis through the use of an ecosystem simulation model driven by remotely sensed data. Global Ecology and Biogeography 13:371-380

Anten NPR (2005) Optimal photosynthetic characteristics of individual plants in vegetation stands and implications for species coexistence. Annals of Botany 95:495-506

Anten NPR, During HJ (2011) Is analysing the nitrogen use at the plant canopy level a matter of choosing the right optimization criterion? Oecologia 167:293-303

Baldocchi DD, Hicks BB, Meyers TP (1988) Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. Ecology 69:1331-1340

Beer C, Reichstein M, Tomelleri E, Ciais P, Jung M, Carvalhais N, Rodenbeck C, Arain MA, Baldocchi D, Bonan GB, Bondeau A, Cescatti A, Lasslop G, Lindroth A, Lomas M, Luyssaert S, Margolis H, Oleson KW, Roupsard O, Veenendaal E, Viovy N, Williams C, Woodward FI, Papale D (2010) Terrestrial Gross Carbon Dioxide Uptake: Global Distribution and Covariation with Climate. Science 329:834-838

Binkley D, Stape JL, Ryan MG (2004) Thinking about efficiency of resource use in forests. Forest Ecology and Management 193:5-16

Björk RG, Ernfors M, Sikström U, Nilsson MB, Andersson MX, Rütting T, Klemedtsson L (2010) Contrasting effects of wood ash application on microbial community structure, biomass and processes in drained forested peatlands. FEMS Microbiology Ecology 73:550-562

Bonan GB (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science 320:1444-1449

Bond BJ, Farnsworth BT, Coulombe RA, Winner WE (1999) Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. Oecologia 120:183-192

Bowman WP, Barbour MM, Turnbull MH, Tissue DT, Whitehead D, Griffin KL (2005) Sap flow rates and sapwood density are critical factors in within- and between-tree variation in CO2 efflux from stems of mature *Dacrydium cupressinum* trees. New Phytologist 167:815-828

Brooks JR, Sprugel DG, Hinckley TM (1996) The effects of light acclimation during and after foliage expansion on photosynthesis of Abies amabilis foliage within the canopy. Oecologia 107:21-32

Canadell JG, Raupach MR (2008) Managing forests for climate change mitigation. Science 320:1456-1457

Cao B, Dang QL, Zhang SR (2007) Relationship between photosynthesis and leaf nitrogen concentration in ambient and elevated CO2 in white birch seedlings. Tree Physiology 27:891-899

Cavaleri MA, Oberbauer SF, Ryan MG (2006) Wood CO2 efflux in a primary tropical rain forest. Global Change Biology 12:2442-2458

Ceschia E, Damesin C, Lebaube S, Pontailler JY, Dufrene E (2002) Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). Annals of Forest Science 59:801-812

Cowan, I.R. and G.D. Farquhar, G.D. 1977. Stomatal function in relation leaf metabolism and environment. In: Jennings, D.H. (Ed.), Integration activity in the higher plant. Cambridge University Press, Cambridge, MA,USA), pp 471–505

Damesin C, Ceschia E, Le Goff N, Ottorini JM, Dufrene E (2002) Stem and branch respiration of beech: from tree measurements to estimations at the stand level. New Phytologist 153:159-172

Day ME (2000) Influence of temperature and leaf-to-air vapor pressure deficit on net photosynthesis and stomatal conductance in red spruce (*Picea rubens*). Tree Physiology 20:57-63

DeLuca TH, Boisvenue C (2012) Boreal forest soil carbon: Distribution, function and modelling. Forestry: In Press

Dewar RC, Franklin O, Makelä A, McMurtrie RE, Valentine HT (2009) Optimal Function Explains Forest Responses to Global Change. Bioscience 59:127-139

Edwards NT, Hanson PJ (1996) Stem respiration in a closed-canopy upland oak forest. Tree Physiology 16:433-439

Ellsworth DS, Reich PB (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96:169-178

Elvir JA, Wiersma GB, Day ME, Greenwood MS, Fernandez IJ (2006) Effects of enhanced nitrogen deposition on foliar chemistry and physiological processes of forest trees at the Bear Brook Watershed in Maine. Forest Ecology and Management 221:207-214

Ernfors M, Rütting T, Klemedtsson L (2011) Increased nitrous oxide emissions from a drained organic forest soil after exclusion of ectomycorrhizal mycelia. Plant and Soil 343:161-170

Evans JR (1989) Photosynthesis and nitrogen relationship in leaves of C-3 plants. Oecologia 78:9-19

Farquhar GD, Caemmerer SV, Berry JA (1980) A biochemical-model of photosynthetic CO2 assimilation in leaves of C-3 species. Planta 149:78-90

Field C (1983) Allocating leaf nitrogen for maximization of carbon gain – leaf age as a control on the allocation program. Oecologia 56:341-347

Fife DN, Nambiar EKS (1997) Changes in the canopy and growth of Pinus radiata in response to nitrogen supply. Forest Ecology and Management 93:137-152

Fredeen AL, Sage RF (1999) Temperature and humidity effects on branchlet gas-exchange in white spruce: an explanation for the increase in transpiration with branchlet temperature. Trees-Structure and Function 14:161-168

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079-1081

Griffin KL, Turnbull M, Murthy R (2002) Canopy position affects the temperature response of leaf respiration in Populus deltoides. New Phytologist 154:609-619

Hall M, Räntfors M, Slaney M, Linder S, Wallin G (2009) Carbon dioxide exchange of buds and developing shoots of boreal Norway spruce exposed to elevated or ambient CO_2 concentration and temperature in whole-tree chambers. Tree Physiology 29:467-481

Han QM, Kawasaki T, Katahata S, Mukai Y, Chiba Y (2003) Horizontal and vertical variations in photosynthetic capacity in a Pinus densiflora crown in relation to leaf nitrogen allocation and acclimation to irradiance. Tree Physiology 23:851-857

Han QM, Kawasaki T, Nakano T, Chiba Y (2004) Spatial and seasonal variability of temperature responses of biochemical photosynthesis parameters and leaf nitrogen content within a Pinus densiflora crown. Tree Physiology 24:737-744

Hermle S, Lavigne MB, Bernier PY, Bergeron O, Pare D (2010) Component respiration, ecosystem respiration and net primary production of a mature black spruce forest in northern Quebec. Tree Physiology 30:527-540

Hikosaka K (2005) Leaf canopy as a dynamic system: Ecophysiology and optimality in leaf turnover. Annals of Botany 95:521-533

Hollinger DY (1996) Optimality and nitrogen allocation in a tree canopy. Tree Physiology 16:627-634

Houghton RA (2005) Aboveground forest biomass and the global carbon balance. Global Change Biology 11:945-958

Jensen KH, Lee J, Bohr T, Bruus H, Holbrook NM, Zwieniecki MA (2011) Optimality of the Munch mechanism for translocation of sugars in plants. Journal of the Royal Society Interface 8:1155-1165

Kellomäki S, Wang KY (1997) Photosynthetic responses of Scots pine to elevated CO2 and nitrogen supply: Results of a branch-in-bag experiment. Tree Physiology 17:231-240

Klemedtsson L, Ernfors M, Björk RG, Weslien P, Rütting T, Crill P, Sikström U (2010) Reduction of greenhouse gas emissions by wood ash application to a Picea abies (L.) Karst. forest on a drained organic soil. European Journal of Soil Science 61:734-744

Klemedtsson L, von Arnold K, Weslien P, Gundersen P (2005) Soil CN ratio as a scalar parameter to predict nitrous oxide emissions. Global Change Biology 11:1142-1147

Knorr W, Heimann M (2001) Uncertainties in global terrestrial biosphere modeling 1. A comprehensive sensitivity analysis with a new photosynthesis and energy balance scheme. Global Biogeochemical Cycles 15:207-225

Kull O (2002) Acclimation of photosynthesis in canopies: models and limitations. Oecologia 133:267-279

Laitinen K, Luomala EM, Kellomäki S, Vapaavuori E (2000) Carbon assimilation and nitrogen in needles of fertilized and unfertilized field-grown Scots pine at natural and elevated concentrations of CO2. Tree Physiology 20:881-892

Lavigne MB, Ryan MG (1997) Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. Tree Physiology 17:543-551

Levy PE, Meir P, Allen SJ, Jarvis PG (1999) The effect of aqueous transport of CO2 in xylem sap on gas exchange in woody plants. Tree Physiology 19:53-58

Limpens J, Berendse F, Blodau C, Canadell JG, Freeman C, Holden J, Roulet N, Rydin H, Schaepman-Strub G (2008) Peatlands and the carbon cycle: from local processes to global implications - a synthesis. Biogeosciences 5:1475-1491

Linderson ML, Mikkelsen TN, Ibrom A, Lindroth A, Ro-Poulsen H, Pilegaard K (2012) Up-scaling of water use efficiency from leaf to canopy as based on leaf gas exchange relationships and the modeled in-canopy light distribution. Agricultural and Forest Meteorology 152:201-211

Liu J, Chen JM, Cihlar J, Park WM (1997) A process-based boreal ecosystem productivity simulator using remote sensing inputs. Remote Sensing of Environment 62:158-175

Lloyd J, Patino S, Paiva RQ, Nardoto GB, Quesada CA, Santos AJB, Baker TR, Brand WA, Hilke I, Gielmann H, Raessler M, Luizao FJ, Martinelli LA, Mercado LM (2010) Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. Biogeosciences 7:1833-1859

Maier CA (2001) Stem growth and respiration in loblolly pine plantations differing in soil resource availability. Tree Physiology 21:1183-1193

Mäkelä A, Givnish TJ, Berninger F, Buckley TN, Farquhar GD, Hari P (2002) Challenges and opportunities of the optimality approach in plant ecology. Silva Fennica 36:605-614

McGuire MA, Teskey RO (2004) Estimating stem respiration in trees by a mass balance approach that accounts for internal and external fluxes of CO2. Tree Physiology 24:571-578

McMurtrie RE, Dewar RC (2011) Leaf-trait variation explained by the hypothesis that plants maximize their canopy carbon export over the lifespan of leaves. Tree Physiology 31:1007-1023

McMurtrie RE, Norby RJ, Medlyn BE, Dewar RC, Pepper DA, Reich PB, Barton CVM (2008) Why is plant-growth response to elevated CO(2) amplified when water is limiting, but reduced when nitrogen is limiting? A growth-optimisation hypothesis. Functional Plant Biology 35:521-534

Medlyn BE, Loustau D, Delzon S (2002) Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (Pinus pinaster Ait.). Plant Cell and Environment 25:1155-1165

Meir P, Kruijt B, Broadmeadow M, Barbosa E, Kull O, Carswell F, Nobre A, Jarvis PG (2002) Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. Plant Cell and Environment 25:343-357

Minkkinen K, Korhonen R, Savolainen I, Laine J (2002) Carbon balance and radiative forcing of Finnish peatlands 1900-2100 - the impact of forestry drainage. Global Change Biology 8:785-799

Minkkinen K, Laine J (2006) Vegetation heterogeneity and ditches create spatial variability in methane fluxes from peatlands drained for forestry. Plant and Soil 285:289-304

Mitchell AK, Hinckley TM (1993) Effects of foliar nitrogen on photosynthesis and water-use efficiency in Douglas fir. Tree Physiology 12:403-410

Monsi M, Saeki T (2005) On the factor light in plant communities and its importance for matter production. Annals of Botany 95:549-567

Mott KA, Peak D (2010) Stomatal responses to humidity and temperature in darkness. Plant Cell and Environment 33:1084-1090

Murthy R, Dougherty PM, Zarnoch SJ, Allen HL (1996) Effects of carbon dioxide, fertilization, and irrigation on photosynthetic capacity of loblolly pine trees. Tree Physiology 16:537-546

Niinemets U, Tenhunen JD (1997) A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species Acer saccharum. Plant Cell and Environment 20:845-866

Pan YD, Birdsey RA, Fang JY, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao SL, Rautiainen A, Sitch S, Hayes D (2011) A Large and Persistent Carbon Sink in the World's Forests. Science 333:988-993

Peak D, Mott KA (2011) A new, vapour-phase mechanism for stomatal responses to humidity and temperature. Plant Cell and Environment 34:162-178

Pereira JS, Chaves MM, Fonseca F, Araujo MC, Torres F (1992) Photosynthetic capacity of leaves of *Eucalyptus globulus* (labill.) growing in the field with different nutrient and water-supplies. Tree Physiology 11:381-389

Plomion C, Leprovost G, Stokes A (2001) Wood formation in trees. Plant Physiology 127:1513-1523

Pruyn ML, Gartner BL, Harmon ME (2002) Within-stem variation of respiration in *Pseudotsuga menziesii* (Douglas-fir) trees. New Phytologist 154:359-372

Ranney TG, Peet MM (1994) Heat tolerance of 5 taxa of birch (*Betula*) – physiological responses to supraoptimal leaf temperatures. Journal of the American Society for Horticultural Science 119:243-248

Rapalee G, Trumbore SE, Davidson EA, Harden JW, Veldhuis H (1998) Soil carbon stocks and their rates of accumulation and loss in a boreal forest landscape. Global Biogeochemical Cycles 12:687-701

Reichstein M, Papale D, Valentini R, Aubinet M, Bernhofer C, Knohl A, Laurila T, Lindroth A, Moors E, Pilegaard K, Seufert G (2007) Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites. Geophysical Research Letters 34

Ryan MG (1990) Growth and maintenance respiration is stems of *Pinus contorta* and *Picea engelmannii*. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 20:48-57

Ryan MG, Gower ST, Hubbard RM, Waring RH, Gholz HL, Cropper WP, Running SW (1995) Woody tissue maintenance respiration of 4 conifers in contrasting climates. Oecologia 101:133-140

Ryan MG, Lavigne MB, Gower ST (1997) Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. Journal of Geophysical Research-Atmospheres 102:28871-28883

Sands PJ (1995) Modeling canopy production .1. optimal distribution of photosynthetic resources. Australian Journal of Plant Physiology 22:593-601

Sellin A (2001) Hydraulic and stomatal adjustment of Norway spruce trees to environmental stress. Tree Physiology 21:879-888

Sellin A, Kupper P (2004) Within-crown variation in leaf conductance of Norway spruce: effects of irradiance, vapour pressure deficit, leaf water status and plant hydraulic constraints. Annals of Forest Science 61:419-429

Sigurdsson BD, Roberntz P, Freeman M, Naess M, Saxe H, Thorgeirsson H, Linder S (2002) Impact studies on Nordic forests: effects of elevated CO2 and fertilization on gas exchange. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 32:779-788

Silvola J, Alm J, Ahlholm U, Nykänen H, Martikainen PJ (1996) CO2 fluxes from peat in boreal mires under varying temperature and moisture conditions. Journal of Ecology 84:219-228

Sprugel DG (1990) Components of woody-tissue respiration in young Abies amabilis (Dougl.) Forbes trees. Trees-Structure and Function 4:88-98

Stenberg P, Kangas T, Smolander H, Linder S (1999) Shoot structure, canopy openness, and light interception in Norway spruce. Plant Cell and Environment 22:1133-1142

Steppe K, Saveyn A, McGuire MA, Lemeur R, Teskey RO (2007) Resistance to radial CO2 diffusion contributes to between-tree variation in CO2 efflux of *Populus deltoides* stems. Functional Plant Biology 34:785-792

Stockfors J (2000) Temperature variations and distribution of living cells within tree stems: implications for stem respiration modeling and scale-up. Tree Physiology 20:1057-1062

Stockfors J, Linder S (1998a) Effect of nitrogen on the seasonal course of growth and maintenance respiration in stems of Norway spruce trees. Tree Physiology 18:155-166

Stockfors J, Linder S (1998b) The effect of nutrition on the seasonal course of needle respiration in Norway spruce stands. Trees-Structure and Function 12:130-138

Talhelm AF, Pregitzer KS, Burton AJ (2011) No evidence that chronic nitrogen additions increase photosynthesis in mature sugar maple forests. Ecological Applications 21:2413-2424

Terashima I, Araya T, Miyazawa S, Sone K, Yano S (2005) Construction and maintenance of the optimal photosynthetic systems of the leaf, herbaceous plant and tree: an eco-developmental treatise. Annals of Botany 95:507-519

Teskey RO, McGuire MA (2002) Carbon dioxide transport in xylem causes errors in estimation of rates of respiration in stems and branches of trees. Plant Cell and Environment 25:1571-1577

Turnbull TL, Kelly N, Adams MA, Warren CR (2007) Within-canopy nitrogen and photosynthetic gradients are unaffected by soil fertility in field-grown Eucalyptus globulus. Tree Physiology 27:1607-1617

Uddling J, Pleijel H, Karlsson PE (2004) Measuring and modelling leaf diffusive conductance in juvenile silver birch, *Betula pendula*. Trees-Structure and Function 18:686-695

Uddling J, Teclaw RM, Pregitzer KS, Ellsworth DS (2009) Leaf and canopy conductance in aspen and aspen-birch forests under free-air enrichment of carbon dioxide and ozone. Tree Physiology 29:1367-1380

Wallin G, Linder S, Lindroth A, Räntfors M, Flemberg S, Grelle A (2001) Carbon dioxide exchange in Norway spruce at the shoot, tree and ecosystem scale. Tree Physiology 21:969-976

Warren CR, Adams MA (2001) Distribution of N, Rubisco and photosynthesis in Pinus pinaster and acclimation to light. Plant Cell and Environment 24:597-609

Warren CR, Adams MA (2004) Evergreen trees do not maximize instantaneous photosynthesis. Trends in Plant Science 9:270-274

Weng ES, Luo YQ, Gao C, Oren R (2011) Uncertainty analysis of forest carbon sink forecast with varying measurement errors: a data assimilation approach. Journal of Plant Ecology-Uk 4:178-191

Weslien P, Klemedtsson AK, Börjesson G, Klemedtsson L (2009) Strong pH influence on N(2)O and CH(4) fluxes from forested organic soils. European Journal of Soil Science 60:311-320

Zha TS, Kellomäki Z, Wang KY, Ryyppö A, Niinistö S (2004) Seasonal and annual stem respiration of Scots pine trees under boreal conditions. Annals of Botany 94:889-896

Zha TS, Wang KY, Ryyppö A, Kellomäki S (2002) Needle dark respiration in relation to within-crown position in Scots pine trees grown in long-term elevation of CO2 concentration and temperature. New Phytologist 156:33-41

Acknowledgements