Realia et naturalia

PILLE MÄND

Light use capacity and carbon and nitrogen budget of plants: remote assessment and physiological determinants

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers which are referred to in the text by Roman numerals:

I   Beier C, Emmett BA, Tietema A, Schmidt IK, Peñuelas J, Kovács Láng E, Duce P, De Angelis P, Gorissen A, Estiarte M, de Dato GD, Sowerby A, Kröel-Dulay G, Lellei-Kovács E, Kull O, **Mänd P**, Petersen H, Gjelstrup P, Spano D. 2009. Carbon and nitrogen balances for 6 shrublands across Europe. *Global Biogeochemical Cycles* 23: 1–13.

II   **Mänd P**, Hallik L, Peñuelas J, Nilson T, Duce P, Emmett BA, Beier C, Estiarte M, Garadnai J, Kalapos T, Schmidt IK, Kovács-Láng E, Prieto P, Tietema A, Westerveld JW, Kull O. 2010. Responses of the reflectance indices PRI and NDVI to experimental warming and drought in European shrublands along a north–south climatic gradient. *Remote Sensing of Environment* 114: 626–636.

III   **Mänd P**, Hallik L, Peñuelas J, Kull O. 2013. Electron transport efficiency at opposite leaf sides: effect of vertical distribution of leaf angle, structure, chlorophyll content and species in a forest canopy. *Tree Physiology* 33: 202–210.

IV   Eichelmann H, Oja V, Rasulov B, Padu E, Bichele I, Pettai H, **Mänd P**, Kull O, Laisk A. 2005. Adjustment of leaf photosynthesis to shade in a natural canopy: reallocation of nitrogen. *Plant, Cell and Environment* 28: 389–401.

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The participation of the author in preparing the listed publications is as follows:
Paper I –   collected and analysed part of the data and participated in writing;
Paper II –   collected and analysed the data and was leading author in writing the paper;
Paper III –   collected and analysed the data and was leading author in writing the paper;
Paper IV –   collected and analysed part of the data and participated in writing.

LIST OF TERMS AND ABBREVIATIONS

abaxial side of leaf	the lower side (usually) of a bilateral leaf, which is often exposed to lower levels of light than leaf adaxial side
adaxial side of leaf	the upper side (usually) of a bilateral leaf, which is often exposed to higher levels of light than leaf abaxial side
APAR	annually absorbed photosynthetically active radiation ($MJ\ m^{-2}\ yr^{-1}$)
carboxylation capacity	the maximum rate of CO_2 fixation of photosynthesis ($\mu mol\ m^{-2}\ s^{-1}$)
Chl a/b	the ratio of concentrations of chlorophyll a to chlorophyll b
Chl b	chlorophyll b
chlorophyll fluorescence	fluorescent light that has been re-emitted after being absorbed by the chlorophyll molecules of a plant
Chl$_s$	chlorophyll content per unit leaf area ($\mu mol\ m^{-2}$)
fAPAR	the fraction of photosynthetically active radiation absorbed by vegetation
far-red irradiation	the red end of the visible light spectrum, wavelength region of 700–800 nm
fluorescence	the emission of light by a substance that has absorbed light, here used in the meaning of chlorophyll fluorescence
F_v/F_m	quantum yield of PSII of dark adapted (relaxed) leaves, calculated as the proportion of absorbed quanta, used in photochemical reactions
GPP	gross primary production, calculated as annual uptake of carbon by vegetation per unit ground area ($g\ C\ m^{-2}\ yr^{-1}$)
green LAI	leaf area index of green plant parts, calculated as leaf area per unit ground area ($m^2\ m^{-2}$)
green LAI$_e$	effective projected green leaf area, calculated as the average number of contacts of inserted pin (pinpoint method) with green plant parts (leaves and green branches)
LAI	leaf area index, calculated as leaf area per unit ground area ($m^2\ m^{-2}$)
LAI$_e$	effective projected leaf area, calculated as average number of contacts of inserted pin (pinpoint method) with plant parts
LHC	light harvesting complex, a complex of proteins and photosynthetic pigments focusing light energy to the reaction centre of the photosystem

LHCI	LHC focusing light energy to the reaction centre of PS I
LHCII	LHC focusing light energy to the reaction centre of PS II
LHCII trimer	large trimeric subunit of LHCII
LMA	leaf dry mass per unit leaf area ($g\ m^{-2}$)
LUE	light use efficiency, defined as the amount of carbon in produced biomass per unit of absorbed light ($g\ C\ MJ^{-1}$)
MODIS	Moderate Resolution Imaging Spectroradiometer acquiring daily reflectance data of Earth's surface
NDVI	Normalized Difference Vegetation Index, acquired from vegetation reflectance at the visible and far-red spectral regions
$NDVI_{570}$	NDVI, calculated from reflectance at 570 and 780 nm
$NDVI_{680}$	NDVI, calculated from reflectance at 680 and 780 nm
N_m	leaf nitrogen content per unit dry mass ($g\ g^{-1}$)
Non-photochemical quenching	mechanism in plants for dissipating excess light energy as heat
NPP	net primary production, calculated as annual production of carbon per unit ground area when carbon cost of respiration is subtracted ($g\ C\ m^{-2}\ yr^{-1}$)
NPQ	non-photochemical quenching, calculated from chlorophyll fluorescence
N_s	leaf nitrogen content per unit leaf area ($g\ m^{-2}$)
PAR	photosynthetically active radiation ($MJ\ m^{-2}\ yr^{-1}$)
photosystem	protein complex that carry out the primary absorption of light and the transfer of energy and electrons during photosynthesis
PPFD	photosynthetic photon flux density, the number of photons in the 400–700 nm waveband incident per unit time on a unit surface ($\mu mol\ photons\ m^{-2}\ s^{-1}$)
PRI	Photochemical Reflectance Index, calculated using reflectance at wavelengths of 531 and 570 nm
PSI	a protein complex that captures and uses light energy to mediate electron transfer from plastocyanin to ferredoxin
PSI antenna	complex of proteins and photosynthetic pigments focusing light energy toward the reaction centre of PS I
PSII	a protein complex that carries out the primary absorption of light in photosynthesis and uses light energy to energize electrons that are then transferred through a variety of coenzymes and cofactors to reduce plastoquinone to plastoquinol

qN	non-photochemical quenching, calculated on a scale of 0–1 from chlorophyll fluorescence
qP	photochemical quenching, an approximation of the proportion of PSII reaction centres that are open, calculated from chlorophyll fluorescence
quantum use efficiency	the proportion of absorbed light that is used in photochemical reactions
red-irradiation	the wavelength region of 600–700 nm of the visible light spectrum
Rubisco	ribulose-1,5-bisphosphate carboxylase-oxygenase, an enzyme catalysing the fixation of CO_2 during photosynthesis
Φ_{II}	quantum yield of PSII of light adapted leaves, calculated as the proportion of light absorbed by PSII that is used in photochemical reactions

1. INTRODUCTION

1.1. Carbon and nitrogen budget of ecosystems

Understanding the determinants of the global carbon cycle is becoming a more and more important task of plant ecophysiology due to predictions of large-scale changes in global climate (IPCC, 2007). Roughly 50 Gt of carbon is annually acquired through photosynthesis just by terrestrial plants (Potter, 2012) and even small changes in climate may cause substantial changes in local scale plant production (Parmesan and Yohe 2003, Peñuelas et al. 2007, Bokhorst et al. 2011). The relationships between vegetation production and irradiance, moisture, temperature and nitrogen, as major limiters of vegetation carbon assimilation, have been studied over different biomes and functional groups and extrapolated to the global scale (e.g. Field et al. 1992, Potter et al. 1993, White et al. 2000, Caylor et al. 2003, Wright et al. 2004, Yuan et al. 2007, Street et al. 2012, Peltoniemi et al. 2012). However, compared to abundant studies on forests and grasslands, very few papers on the carbon balances of shrublands are available, although this data is also needed for the determination of global carbon budgets.

In parallel with studies on carbon budget of different ecosystems, more and more attention is paid also to nitrogen content of plants. Already in 1987 Hirose and Weger demonstrated that nitrogen distribution has a strong effect on daily canopy carbon gain, and plants from a denser stand should benefit more from the nonuniform distribution of nitrogen in the canopy (Hirose 2005). Therefore it was assumed that the modelling of canopy photosynthesis with leaf nitrogen distribution enables us to scale up from chloroplast biochemistry to canopy carbon gain (Kull and Jarvis, 1995, De Pury and Farquhar, 1997). Recently canopy-scale measurements have also proven the significant effect of the nitrogen budget of ecosystems on canopy carboxylation capacity, respiration and soil turnover rates, all of which control the canopy carbon cycle and influence the sensitivity of the global carbon cycle to changes in climate (Lambers et al. 2008, Ollinger et al. 2008). Thus C/N ratios of different functional types of plants are often incorporated into plant production models (White et al. 2000, Wania et al. 2012). At the same time the whole concept of nitrogen assimilation by plants has changed (Schimel and Bennett 2004) more efficiently explaining the link between carbon and nitrogen budgets. Nevertheless, there are still large disagreements in calculations of global scale nitrogen balance (Zaehle and Dalmonech 2011, Wania et al. 2012) partly due to changes in C/N ratio in plants as a result of changing climate (Sardans et al. 2012) and partly because of a lack of knowledge on the nitrogen cycles of different ecosystems and plant functional types.

Today the main obstacle for modelling global vegetation processes lies in the identification of a minimal number of plant functional types, in order to reduce the complexity of traits that are needed for productivity predictions (Lavorel et al. 2008). On the other hand, to be able to select those relevant traits and plant groups we need enough knowledge on the whole range of natural variability in

different light-capture and light-use parameters and strategies, which determine the productivity. Thus, two different approaches are used for modelling global productivity: ´top-down´ models using remotely sensed data integrate both physiological and structural vegetation parameters, and ´bottom-up´ models scale productivity to the canopy level from the known chloroplast- and leaf-level physiology and its relations to resource availability (Houborg et al. 2009).

1.2. Remote sensing of plant productivity

Often the ´top-down´ approaches are based on interpretations of remotely sensed canopy reflectance signals (Hilker et al. 2008). To detect changes in global plant cover, remote sensing technologies are constantly developing and there is a search for the best remotely estimated fit for key parameters of productivity (Monteith and Moss 1977): leaf area index (LAI), the fraction of photosynthetically active radiation absorbed by vegetation (fAPAR) and the light use efficiency (LUE). Reflectance index NDVI (Rouse et al. 1974) is one remote sensing parameter that is often used as an estimate of the fraction of photosynthetically active radiation absorbed by vegetation (fAPAR) (Huemmrich et al. 2010, Peng et al. 2012, Lausch 2013) and a closely related parameter, green leaf area index (green LAI) (Fensholt et al. 2004, Haboudane et al. 2004). The estimations of fAPAR and LAI have already been improved over a number of years and the best outcome is that based on MODIS algorithm global LAI and fAPAR data at a 1×1 km spatial resolution is collected on regular basis (Myneni et al. 2002). However, MODIS sorts the vegetation within each pixel to one of six given biomes leaving room for misclassifications and similarly to small-scale NDVI measurements, at dense canopies MODIS LAI tends to saturate (Myneni et al. 2002). Differently from fAPAR and LAI, estimations of LUE have been improved most extensively over the last decade as spectrometers with better resolution became available.

In general two different approaches for determining LUE from a distance are used: the first option is the prediction of LUE indirectly from environmental stresses, the other possibility is to predict LUE more-or-less directly from changes in spectral reflectance (Hilker et al. 2008). The environmental-stress based LUE estimations using narrow waveband reflectance are highly sensitive to atmospheric scattering and direction of measurements (Liu et al. 2006), yet recently hyperspectral imagery has quite successfully been used for prediction of foliage nitrogen content from narrow waveband reflectance (Martin et al. 2008, Ollinger et al. 2008). The MODIS project also gives estimates of GPP, which use biome-specific information about stress-induced changes in maximum LUE (Heinsch et al. 2003), even though several studies have reported LUE to vary not only between biomes but also between different functional groups of species (Nichol et al. 2000, Ahl et al. 2004, Kergoat et al. 2008).

The alternative approach is estimating LUE more directly from spectral reflectance, for instance by measuring solar induced chlorophyll fluorescence emissions of canopies, or more precisely the impact of fluorescence emissions on apparent spectral reflectance (Zarco-Tejada et al. 2000, Moya et al. 2004). However, this approach has been technically tricky since right now, remote detection of chlorophyll fluorescence is possible only by using sub-nanometre reflectance bands in the red and near infrared regions where solar radiation is not abundant (Meroni and Colombo 2006). Concurrently remotely sensed changes in the photoprotective mechanism are also used for estimations of canopy LUE, since a reflectance index PRI has been proposed as an optical proxy of light use efficiency (Garbulsky et al. 2011). Using a reflectance band at 531 nm, reflectance index PRI involves combined information on changes in the xanthophyll cycle and the aggregation state of PSII antennas (Gamon et al. 1992, Peñuelas et al. 1995, Gamon et al. 1997). For measurements from space the relationship between LUE and PRI is better if an atmospherically corrected band of 678 nm is used for PRI calculations, and PRI measurements from space seem to improve MODIS LUE derivations immensely when compared to the previously-used biome-specific look-up table of maximum LUEs (Drolet et al. 2008). Yet, the relationship between PRI and LUE seems to be species-specific, much less variance in LUE is described by PRI when different functional types of plants are investigated (Garbulsky et al. 2011). Also the reliance of PRI on canopy structure and light conditions has been reported (Barton and North 2001, Grace et al. 2007, Hilker et al. 2008). Thus the applicability of PRI for estimation of LUE of different ecosystem types with varying canopy structure still needs to be tested.

1.3. The effect of canopy structure on estimations of light use efficiency

Currently one of the most challenging aspects of remote sensing is tracking the photosynthetic activity of forests, since the remote estimation of carbon uptake by multilayered forest ecosystems involves several difficulties (Grace et al. 2007). The structure dependence of PRI values applies also to the vertical structure of vegetation (Nichol et al. 2000, Barton and North 2001, Damm et al. 2010). Forests, as very complex systems of coexisting species with different spatial and temporal strategies for light capture may as a whole system in fact be much more efficient in light use than simpler canopy-systems (Ishii and Asano 2010). For instance the productivity of the whole ecosystem appears to be higher in mixed forests, which consist of both broadleaved and coniferous species (Aiba et al. 2007). Mostly the ´top-down` models using reflectance data for estimations of light use efficiency, are very simple. Nevertheless simple LUE models may perform even better than more detailed ´bottom-up` scaled-leaf models containing several species-specific parameters (Houborg et al.

2009). It is difficult to obtain enough input data for multilayer models in order to derive total canopy-scale fluxes.

However, to understand the mechanistic basis of changes in leaf and canopy-level light use, more complex models are necessary. Multilayer models that consider the vertical variability of photosynthesis or at least divide canopy into shaded and sunlit fractions have proven to better estimate the diurnal changes in canopy photosynthesis (Chen et al. 1999, Baldocchi and Wilson, 2001, Damm et al. 2010). Among other factors that influence canopy photosynthesis, the efficiency with which leaf canopy is exposed to light is shown to be a function of inclination angles and spatial aggregation of leaves (Cescatti and Niinemets 2004, Niinemets 2010). However, simpler models assume the inclination angle distribution of plant canopies to be spherical, even if such a generalization may cause significant bias in the estimations of vertical distribution of light and photosynthesis within the canopy (Stadt and Lieffers 2000, Sarlikoti et al. 2011). This is because real vegetation canopies consist of a mixture of species with several alternative leaf inclination distributions (Niinemets 2010).

Another topic that needs to be studied more explicitly is the physiological relationship between leaf level chlorophyll fluorescence measurements and CO_2 assimilation, as there are indications that this relationship may change among leaves with different inclination angles and resultant light conditions (Myers et al. 1997, Tsuyama et al. 2003, Damm et al. 2010). This suggests that if estimations of leaf level quantum use efficiency derived from chlorophyll fluorescence are used for modelling canopy photosynthesis, the inclusion of leaf angle distribution into the model may be necessary. Most probably, leaf-level differences in light acclimation strategies also influence the upscaling from leaf-level quantum use efficiency to canopy light use efficiency (Damm et al. 2010).

1.4. Within-leaf mechanisms influencing light-use efficiency

In order to understand the factors influencing the up-scaling of photosynthetic properties from leaf to canopy the variations in leaf structure and the differences in light-acclimation of chloroplasts within the leaf must be considered. The leaf and chloroplast properties that define light use efficiency of the whole canopy have been studied profoundly (Kull 2002), but the magnitude of these light induced changes in leaf morphology and physiology is not known for different environmental conditions and for different species or functional groups (Ishii and Asano 2010). Valladares and Niinemets (2008) concluded that the magnitude of light acclimation of leaf morphology is larger in shade tolerant species, whereas high-light demanding species change their physiology more plastically. However, the morphology of shade tolerant species can not be the major means of optimizing the quantum use of sunfleck energy, which is one factor strongly influencing the carbon gain of lower canopy regions (Porcar-Castell and Palmroth 2012, Way and Pearcy 2012). Furthermore, the regulation of one trait, such

as leaf chlorophyll content, which has been shown to be a very sensitive indicator of different environmental stresses, can be achieved either through changes in the overall percentage of chlorophyll, through physiological redistribution of chlorophyll between different photosynthetical units, but also through changes in leaf morphology as changes in LMA with constant chlorophyll content may affect light capture efficiency significantly (Niinemets 2010).

The distribution of leaf photosynthetic traits through the canopy seems to be controlled not only on the leaf level but is evidently a whole-canopy phenomenon (Givnish 1988, Kull 2002). Indeed, Moreau et al. (2012) found that the relationship between canopy nitrogen gradient and the corresponding light gradient is a function of canopy size. Yet, changes in leaf nitrogen have proven to be of key importance in the acclimation of leaf photosynthesis to different light conditions (Hirose 2005). In fact, the photosynthetic performance of leaf and canopy is defined not only by within leaf and canopy nitrogen distribution, but also the magnitude of changes in different leaf traits depends on the availability of resources, such as nitrogen (Portsmuth and Niinemets 2007). The reason behind the nitrogen dependence of chlorophyll content and distribution is that chlorophylls need to be bound to proteins that are costly since they contain nitrogen (Evans 1989). The magnitude of light adjustment of the photosynthetic apparatus is not only restricted by the availability of resources (such as nitrogen), but there probably also exists a lower limit of acclimation, as certain constructional features define the minimum amount of nutrients for photosynthetic units to remain intact and active (Kull 2002, Meir et al. 2002).

The consideration of chloroplast-level light acclimation differences within the leaf have not been very common in ecological studies as many gaps are still present in the knowledge of the molecular-level adjustment of photosynthetic compounds to irradiance. Due to technical limitations the differentiation between photosynthetic subunits and the detection of the allometric redistribution of different components of the photosynthetic apparatus *in situ* in leaves from natural canopies has not been possible until recently. That is why the acclimation of the photosystem has remained relatively unnoticed until advances in state transition studies have stressed the variability in light harvesting abilities of PSI (Ruban et al. 2006, Ruban and Johnson 2009, Minagawa 2011). Traditionally a lot of attention has been paid to the light adjustment of photosystem II since in ecological research, leaf chlorophyll a/b ratio has often been observed to decrease with decreasing light availability and has been interpreted as a proportional increase in the chlorophyll b binding light harvesting complex of LHCII complexes (Evans 1989). However, studies on the molecular-scale light acclimation of photosystem II implicate multiple locations for chlorophyll b (Ruban et al. 2006, Kouřil et al. 2013).

In addition to light acclimation of photosystems, other nitrogen-rich units of the photosynthetic apparatus, such as ribulose-bisphosphate carboxylase-oxygenase (Rubisco), are also subjected to changes in light environment. It has been shown that in high-light species the investment of nitrogen into carboxylation enzymes, rather than into chlorophyll, increases photosynthetic

capacity more efficiently (Niinemets and Tenhunen 1997, Terashima et al. 2006). The inclusion of parameters considering light-acclimation-induced changes in the allocation of protein between different components of photosynthesis could improve the predictions of maximum photosynthetic capacity of photosynthesis models (Mott and Woodrow 2000, Porcar-Castell and Palmroth 2012). Nevertheless, too little is known about the natural variability in the amount of Rubisco and other units of photosynthetic apparatus across several species and plant functional groups in order to construct mechanistic models linking nitrogen allocation to electron transport, carboxylation, respiration, storage and light use efficiency (Xu et al. 2012).

1.5. Aims of the thesis

The general aim of this study was to investigate the factors that influence primary production of vegetation and remote estimations of primary production, focusing on the most variable component of primary production – light use efficiency. In particular, we studied which factors are most responsive to changes in leaf and canopy light environment and how do these differences in canopy, plant and leaf architecture and physiology influence optical estimations of leaf- and canopy-level light use capacity and the green leaf area index (green LAI). First, based on previous knowledge of the dependence of remote estimations of vegetation physiology on the wavelength region from where optical signals are obtained, we assumed that measurements from the region of maximum absorption of chlorophyll might be worse estimators of plant properties than measurements from wavelength region where chlorophyll absorption is weaker. Secondly, we expected that canopy reflectance index PRI is well suited for estimating canopy light-use efficiency in European shrublands. We also assumed that the fraction of whole-leaf light capture efficiency that is described by optical measurements of chlorophyll fluorescence, changes within the vegetation canopy as a function of leaf angles, since differences in leaf orientation cause larger or smaller irradiance differences between alternate sides of a bilateral leaf. Additionally we expected that canopy and leaf nitrogen content adjusts more extensively to differences in light conditions than light-absorbing chlorophyll content.

The specific objectives of this thesis were:
1. To produce an integrated scheme of carbon and nitrogen pools and fluxes of European shrublands.
2. To estimate the applicability of reflectance indices NDVI (calculated from two different wavelength regions) and PRI in estimating green LAI and light use efficiency of different shrubland communities that are subjected to varying conditions of irradiance, precipitation and temperature.

3. To investigate the effect of canopy and leaf structure on remote estimations of canopy-level light-use efficiency and leaf-level quantum capture efficiency.
4. To search for differences in leaf chlorophyll distribution within leaves from different canopy positions and different species.
5. To study the natural variation in the fraction of photosynthetic and non-photosynthetic nitrogen in leaves from different irradiance conditions and different species.
6. To find out if canopy nitrogen content can be used for estimating differences in carbon production of aboveground vegetation of European shrublands.

2. MATERIALS AND METHODS

2.1. Study sites and experimental set-up

Field studies were carried out at two different spatial scales. A large-scale manipulation experiment of European shrublands differing in annual irradiation, moisture and temperature has been described in **I** and **II**. The steep vertical canopy light gradient of a multi-layered deciduous forest at Järvselja, Estonia, was investigated in **III** and **IV**.

Papers I and II

The experimental sites of six European shrublands were located in Wales-UK, Denmark, Netherlands, Hungary, Sardinia-Italy, and Catalonia-Spain where next to three control plots, three repetitions of warming and drought systems were installed in order to imitate changed climate. In warming experiment the vegetation was covered with reflective curtains at night: this decreased the loss of heat and increased soil temperature by 0–3 °C, depending on the site. For drought treatments, during precipitation the vegetation was covered with transparent waterproof covers for two-month periods within the growing season, reducing the precipitation of year 2003 by 39–349 mm, depending on the site. This experiment was part of EU projects CLIMOOR and VULCAN (Beier et al. 2004). The meteorological survey and measurements for canopy belowground and aboveground carbon and nitrogen pools and fluxes were performed during the years 1998–2004 for **I**. Optical measurements of **II** were carried out in summer 2003, in a period when drought treatment was being applied at each site. During both studies, air and soil temperature, precipitation and irradiance were constantly recorded by permanent sensors.

In **I** the aboveground vegetation structure and frequency (pinpoint measurements), carbon and nitrogen content of plant tissue and litter, litter decomposition rate, belowground root length, soil carbon and nitrogen content at main rooting depth and in mineral soil, the carbon content of microbial biomass, soil respiration, concentrations of NO_3 and NH_4 in soil, NO_3^- and dissolved organic carbon (DOC) concentration in soil water were measured in order to calculate plant biomass, root litterfall, the decomposition of soil organic matter, the fraction of autotrophic and heterotrophic soil respiration, nitrogen mineralization rate, soil water balance, leaching losses of NO_3^- and DOC and eventually the carbon and nitrogen pools and fluxes of different shrubland ecosystems.

In **II** canopy reflectance, chlorophyll fluorescence, concentration of leaf chlorophyll, leaf mass per area (LMA) and leaf nitrogen content were measured. Canopy reflectance measurements and part of the leaf-level fluorescence measurements of **II** were performed on the same subplots as measurements of canopy structure (pinpoint measurements) of **I**. Canopy reflectance was measured using a ground-based S2000-FL spectrometer (Ocean Optics Inc., Dunedin, FL, USA) from the spectral region between 400 nm and 950 nm at 1 m height

above the canopy, and vegetation indices PRI and $NDVI_{680}$ and $NDVI_{570}$ were calculated. See more details in **I** and **II**.

Papers III and IV

The experiments were performed in Estonia at Järvselja Experimental forest (58°22´N, 27°20´E) in the summers of 1999–2002. Permanent scaffholding towers were used to access the topmost and lowest canopy layers of the studied tree species: shade intolerant *Betula pendula* Roth. and *Populus tremula* L. and shade tolerant subcanopy *Tilia cordata* Mill. In **IV**, a herbaceous species *Solidago virgaurea* was also taken under examination. Above each measured leaf light conditions were estimated by using hemispherical photography.

In **III**, chlorophyll fluorescence from the adaxial and abaxial side of the leaf, leaf concentrations of chlorophyll a and b, LMA, and leaf angles were measured. Leaf adaxial/abaxial fluorescence ratios were used as estimations of varying intraleaf light acclimation profiles of chloroplasts. In the following year, leaf reflectance from the wavelength range of 655–665 nm (red spectral region) and 550–560 nm (green spectral region), LMA and leaf chlorophyll content and nitrogen content were measured at the same canopy heights of the same trees where the fluorescence measurements of previous year had been carried out. We measured leaf transmittance and reflectance with an integrating sphere (ISP-80-8-R, Ocean Optics) and fibre optic spectrophotometer (S2000, Ocean Optics).

In **IV**, shoots of *B. pendula* and *T. cordata* were cut and immediately placed into water, while the herbaceous species *S. virgaurea* was dug up and planted into pots with moist soil. For non-destructive measurements of partial reactions of photosynthesis a combined gas exchange/optical system was used in order to simultaneously measure quantum flux densities and chamber CO_2 and O_2 concentrations and to record CO_2 uptake, O_2 evolution, chlorophyll fluorescence, and 820 nm absorptance (Laisk et al. 2002, Eichelmann et al. 2004). In addition we measured chlorophyll a and b content, concentration of proteins (including Rubisco), leaf dry weight and area and leaf nitrogen concentration. Data was used for calculations of PSII quantum capture efficiency and PSII e^- transport rate, relative optical cross-section of PSII, relative absorption cross-section of PSI, densities of PSII and PSI and antenna sizes of PSII and PSI and the mass of nitrogen in different photosynthetic compartments. See more details in **III** and **IV**.

Leaf chlorophyll fluorescence of was measured using modulated chlorophyll fluorescence equipment PAM-2000 (WalzGmbH, Effeltrich, Germany) at both study-sites. See more details in **II–IV**.

2.2. Data processing

Total ecosystem C balance ($\Delta_{\text{C-System}}$) at **I** was calculated as:

$$\Delta_{\text{C-System}} = \text{Dep}_{\text{DOC}} + \text{NPP} - \text{Soilresp}_{\text{Het}} - \text{C-Leach}_{\text{DOC}} \tag{1}$$

where Dep_{DOC} is deposition of carbon into soil as dissolved organic carbon (g C m^{-2} y^{-1}), NPP is net uptake of carbon by plants (g C m^{-2} y^{-1}), Soilresp$_{\text{Het}}$ is carbon used in heterotrophic soil respiration (g C m^{-2} y^{-1}), Leach$_{\text{DOC}}$ accounts for losses in dissolved organic carbon through leaching (g C m^{-2} y^{-1}). See more details in **I**.

Effective projected leaf area (green LAI_e) of shrublands at **II** was calculated as the average number of contacts with green parts (leaves and green branches) of the plants per pin. See further details in **II**.

The vegetation reflectance indices at **II** were calculated as follows:

$$\text{NDVI}_{680} = (R780 - R680)/(R780 + R680) \tag{2}$$
$$\text{NDVI}_{570} = (R780 - R570)/(R780 + R570) \tag{3}$$
$$\text{PRI} = (R531 - R570)/(R570 + R531) \tag{4}$$

Rx in the equations is the reflectance at x nm. For more details of canopy reflectance measurements see details in **II**.

Leaf-level reflectance parameters for alternate leaf sides of deciduous trees at **III** were averaged from the red spectral region (655–665 nm) and the green spectral region (550–560 nm). Sample absorption at the same wavelength ranges was calculated from the equation:

$$\text{absorptance} = (1 - \text{reflectance} - \text{transmittance}) \tag{5}$$

Leaf-level chlorophyll fluorescence parameters, such as quantum yield of PSII of dark-adapted leaves (F_v/F_m) and light-adapted leaves (Φ_{II}), photochemical quenching (qP) and non-photochemical quenching (NPQ and qN) in **II–IV** were calculated from equations:

$$\Phi_{\text{II}} = (F_m` - F)/F_m` \tag{6}$$
$$F_v/F_m = (F_m - F_o)/F_m \tag{7}$$
$$qP = (F_m` - F)/(F_m` - F_o`) \tag{8}$$
$$\text{NPQ} = (F_m - F_m`)/F_m` \tag{9}$$
$$qN = (F_m - F_m`)/(F_m - F_o) \tag{10}$$

where F_o is minimum fluorescence yield and F_m maximal fluorescence yield of dark-adapted leaves. $F_m`$ is maximal fluorescence yield and $F_o`$ minimum fluorescence yield of light-adapted leaves. See further details in **II–IV**.

The relative absorption cross-section of PSII (a_{II}) and PSI (a_{I}) and antenna sizes of PSII (PSUII) and PSI (PSUI) in **IV** were calculated as follows:

$$a_{II} = Yc/\Phi_{II} \tag{11}$$
$$a_I = Yc/Y_p \tag{12}$$
$$Y_p = P_o–P_s/P_m \tag{13}$$
$$PSUI = (a_I/a_I+a_{II})Chl/N_I \tag{14}$$
$$PSUII = (a_{II}/a_I+a_{II})Chl/N_{II} \tag{15}$$

where Yc is quantum yield of linear electron transport, calculated from the photosynthetic carbon metabolism, P_m is the transmittance signal at 820 nm that corresponds to totally oxidized PSI, P_o is the pulse-oxidizable fraction of PSI, P_s is the transmittance signal corresponding to the steady-state oxidation of PSI, N_I is the density of PSI, and N_{II} is the density of PSII. N_{II} was determined as four times the oxygen evolution from a saturating single-turnover flash. Two different kinetic methods were used for determining N_I, see **IV** for details. Chl is the fraction of total chlorophyll that is bound to a certain photosystem. Total Chl was assumed to be distributed between the photosystems proportionally with a_{II} and a_I. The mass of nitrogen in the cores of PSI and PSII in **IV** was calculated from the measured N_I and N_{II}.

For more information about the calculation of different plant parameters see details in **I**–**IV**.

Light use efficiency:
For this thesis we calculated the light use efficiency, LUE (g C MJ^{-1}), of six European shrublands from a simple equation (Monteith 1972, Montieth and Moss 1977):

$$LUE = NPP/APAR \tag{16}$$
$$APAR = PAR \times fAPAR \tag{17}$$

We used net primary production NPP (kg C m^{-2} yr^{-1}) estimations for different European shrublands, which were calculated as described in **I**. APAR was absorbed photosynthetically active radiation (MJ m^{-2} yr^{-1}), which was calculated from PAR (photosynthetically active radiation, MJ m^{-2} yr^{-1}) multiplied by green fAPAR (fraction of PAR absorbed by green vegetation canopy). fAPAR was calculated as a function of LAI (Ruimy et al. 1999):

$$fAPAR = 0.95 \times (1–e^{-k \times LAI}) \tag{18}$$

For the light extinction coefficient (k) a default value of 0.5 (Campbell and Norman 1998) was used. LAI was measured by the pin-point method (Jonasson 1988, description at **II**) where we assumed LAI to be robustly half of the average number of contacts with a plant per pin (LAIe):

$$LAI = 0.5 \times LAIe \tag{19}$$

A different index for estimating LUE of shrublands was derived from a paper by Green et al. (2003), where the strongest predictor of LUE across all data appeared to be an index using nitrogen content of leaves:

$$Index_{LUE} = (LAI \times N_m/100)/fAPAR \qquad (20)$$

where N_m was obtained from the average nitrogen content of the leaves of the dominant species.

Statistical analysis:
For statistical analysis we used STATISTICA software (StatSoft Inc. USA). Linear and nonlinear regression analysis were used in **I**, **II** and **IV** for analysing the effect of differences in climate and irradiance on mean ecosystem parameters of different study-sites, for estimating light use efficiency of leaves from reflectance parameters and for finding the best fit of relationships between different ecosystem, canopy and leaf parameters. Multiple regression analysis was performed to estimate different light use parameters from reflectance indices measured above plants in **II**. Pearson´s correlation in **II** and **IV** or Spearman correlation coefficients in **III** (in the case of heteroscedasticity) were calculated between various leaf and canopy parameters. The normality and homoscedasticity of data was tested. Logaritmic transformation was performed if deviation from normal distribution was found. General linear models (GLM) were constructed in **II,** considering different categorical and continuous predictors. The squared component of a continuous factor was included in the models if the tested variable was nonlinearly related to a given factor. The significance of differences between separate groups was investigated using the Fisher LSD post-hoc test in **II** and **IV**. Non-parametrical Kruskal–Wallis ANOVA by ranks was used for analysing the data in **III,** due to heteroscedasticity. For testing the significance of differences between species in **III,** Wilcoxon signed rank test was used. In **IV** the significance of differences between shade and sun leaves was tested using the *t*-test for independent groups. See more details about statistical analysis in **I–IV**.

3. RESULTS AND DISCUSSION

3.1. Primary production of shrublands

In order to remotely estimate and model changes in shrubland production we first need data on a varying range of carbon storage rates/fluxes and biochemical cycles of different shrublands, since not many papers about the carbon budgets of shrublands have been published. Our studies at six different sites in Europe revealed that apparently similar shrubland ecosystems range from being carbon sinks in moist areas (system uptake 126 g C m^{-2} y^{-1} in Wales) to carbon sources in more arid regions (system emission up to 536 g C m^{-2} y^{-1} in non-steady-state Italian shrubland) (Fig. 4 in **I**).

Models of the global carbon cycle have demonstrated that in forest ecosystems, belowground carbon allocation is one of the largest fluxes of C aside from canopy assimilation (Davidson et al. 2002). Our study (**I**) revealed that steady-state shrubland systems appear to allocate even larger amounts of carbon belowground relative to litterfall (an average of 5:1) compared to most forest systems (2:1) as shown by Davidson et al. (2002). We also found that differences in carbon allocation of various European shrublands could not be explained by differences in annual temperature or precipitation, even if the non-steady-state shrubland of Italy was left out of the analysis (Fig. 1). Neither did mean annual radiation explain differences in carbon allocation (data not shown).
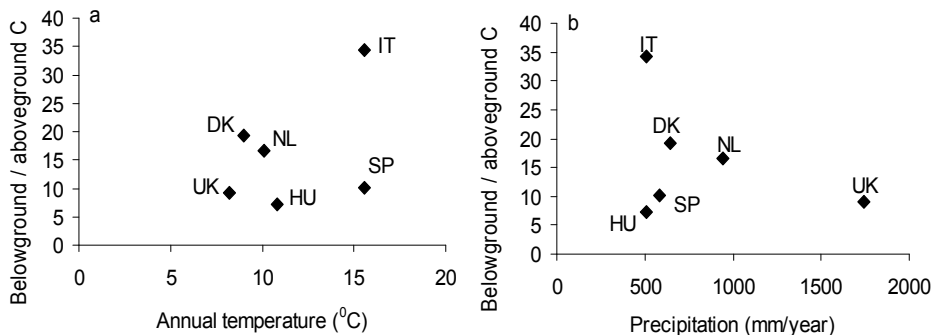
Figure 1. Ratio between belowground and aboveground carbon content related to (a) mean annual temperature and (b) mean annual precipitation at six European shrublands. High ratios in Italy result from the early successional stage of the shrubland after clearcut.

As a result, we expected that large belowground C fluxes of shrublands make it difficult to detect changes in the carbon balance of shrublands by remote-sensing tools, as this method deals only with parameters that can be measured aboveground. However, the aboveground carbon of different shrublands showed a significant exponential relationship to mean annual precipitation (Fig.

2b in **I**). Higher precipitation increased also the quantum absorbing area of vegetation, green LAI_e (Fig. 1a in **II**). Despite site-specific allocational differences in carbon pools, our measurements at five European shrublands suggest that at a large scale, aboveground carbon pools of shrublands are likely to be related (though according to five studied shrublands the relationship might be non-linear) to belowground carbon pools in steady-state shrublands (Fig. 1a in **I**), assuring that robust assumptions about belowground carbon pools can be made based on aboveground or above canopy measurements.

3.2. Green LAI of shrubland communities, estimated by NDVI

If we intend to estimate carbon pools and fluxes from a distance, we can not deal just with allocational differences, but must also consider that canopy structure and background properties affect our estimations (Barton and North 2001, Grace et al. 2007, Hall et al. 2008, Hilker et al. 2010). Our measurements of reflectance index $NDVI_{680}$ at six European shrublands revealed a positive relationship between NDVI and green LAI_e (effective green leaf area index). However this relationship tended to saturate at medium to high green LAI_e conditions (Fig. 4 in **II**, Table 4 in **II**). Similar levelling off of NDVI at dense vegetation has been reported in different vegetation types at multiple spatial scales (Gamon et al. 1995, Myneni et al. 2002, Haboudane et al. 2004, Lausch 2013). Thus, our result indicates that $NDVI_{680}$, which is calculated using red spectral region near maximum absorbtance of chlorophyll, cannot be used for detecting changes in green LAI in dense shrublands.

In order to lessen the saturation effect of $NDVI_{680}$, we additionally calculated $NDVI_{570}$, which used green spectral region (less absorbed by chlorophyll). Although, at northern sites, relationships between $NDVI_{570}$ and green LAI_e or fluorescence parameters were slightly stronger than the same relationships with $NDVI_{680}$ (Table 5 in **II**), saturation of $NDVI_{570}$ still occurred in denser vegetation (Fig. 4 in **II**). However, a recent multi-scale study with different spectrometers gives hope that NDVI calculated from the green spectral region can also be used at higher LAI conditions if the methodology is improved (Lausch 2013).

While testing NDVI for detecting the effect of drought and night-time warming on shrubland vegetation, we found that generally lower values of NDVI were recorded in drought treatment plots (mean effect at Fig. 2 in **II**). On the other hand, if we searched for treatment effects at different study-sites separately, we found no significant drought effect on NDVI, and the warming treatment significantly increased NDVI only in the Italian site (Fig. 2 in **II**). As the treatments simulated realistic climate changes (being realistically small), the possible changes in green LAI_e were not large either and we found green LAI to be significantly affected by manipulations just in Denmark, where artificial drought significantly decreased green LAI_e (Fig. 2 in **II**). In fact, green LAI and related parameter fAPAR may not react too quickly to small changes in en-

vironmental conditions. The additional component of primary production – LUE, on the other hand, is highly variable and has been shown to respond strongly to different environmental changes (Gamon et al. 1997, Guo and Trotter 2004, Ahl et al. 2004, Hilker et al. 2012).

## 3.3. LUE of shrubland communities, estimated by PRI

Recently Garbulsky et al. (2011) reviewed studies where the relationship between remotely sensed vegetation index PRI and vegetation LUE was tested, and found that, in general, PRI can be used at different spatial scales, from leaves to ecosystems, for estimating changes in vegetation light use efficiency. They showed that PRI may be useful in remote sensing assessment of LUE, since it accounted for between 42 and 67% of the total variance of LUE at all spatial scales from leaves to ecosystems. However, they found the lowest R^2 values for PRI *vs* LUE relationships for shrubland ecosystems.

Our measurements, on the other hand, suggested that PRI can be used for detecting changes in leaf-level quantum use (Fig. 5 in **II**, Table 7 in **II**) and changes in green LAI_e (Fig. 4c in **II**) of dense shrublands, however additional data on shrublands with different productivity would be useful for more conclusive results. We also calculated two different estimations of LUE using data from direct measurements on the ground for separate shrublands and we found that PRI correlated with an index of LUE (Fig. 2c), which is a function of canopy nitrogen content and LAI (Green et al. 2003). Nevertheless, a significant relationship was not found between LUE (based on NPP estimations) and PRI, however, we had too few shrublands with medium to large LUE and we did not use site-specific light extinction coefficients. As the assumption of spherical leaf angle distribution is often not valid, (an example of actual leaf angle distributions of forest canopy is given in Fig. 2 in **III**), site specific light extinction estimations should be used when calculating LUE (Stadt and Lieffers 2000, Sarlikioti et al. 2011). Both LUE estimations were significantly correlated with each other (Fig. 2c). The low R^2 of LUE-PRI relationship in shrublands in the paper by Garbulsky et al. (2011) is based on data from southern shrublands, as only a few studies on PRI and LUE relationships in shrublands are available.

Our measurements of southern shrublands also revealed that, in sparse vegetation (Fig. 4c in **II**) and brighter soil (Tables 6 and 7 in **II**), PRI is not sensitive enough for detecting differences in vegetation. Indeed, Filella et al. (2004) showed in the sparse southern shrubland of Spain that NDVI followed the seasonal fluctuations in photosynthesis much better than PRI. PRI has also been reported to be a less reliable estimator of photosynthetic activity in severe stress, including drought conditions (Sims et al. 2006, Ripullone et al. 2011, Porcar-Castell et al. 2012). However, in our experiment with modest drought treatment no significant differences in variances of PRI *vs* quantum use relations were detected when compared to control plots (Fig. 5 in **II**). Even though we did not

detect any effect of artificial drought on PRI (Fig. 2b in **II**), we found that warming treatment generally increased PRI values in shrublands (Fig. 2a in **II**).
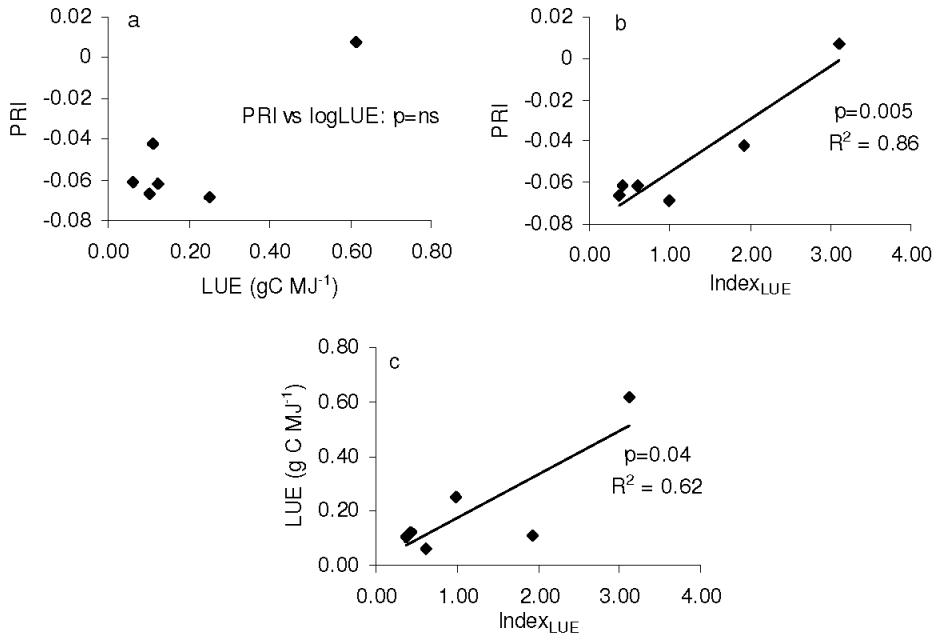
Figure 2. Relationship between two estimations of canopy light-use efficiency and a reflectance index PRI. (a) LUE was estimated using calculations of NPP and LAI (Monteith 1972, Montieth and Moss 1977). (b) Index$_{LUE}$ is a function of nitrogen content of leaves and LAI (Green et al. 2003). p values for significant differences are shown, ns means p>0.05, N=6.

Our study suggests that in modest stress conditions, PRI is more sensitive to changes in the physiological processes of shrubland vegetation than the previously discussed NDVI, since the PRI *vs* green LAI$_e$ relationship was affected by treatments (Table 4 in **II**), unlike the NDVI *vs* green LAI$_e$ relationship. More challenging is the interpretation of the exact physiological mechanism, that influences PRI, as we found no significant treatment effect on leaf-level measurements of quantum capture of PSII (Fig. 5 in **II**), even though PRI was significantly correlated to fluorescence-based quantum use efficiency, since the largest part of the variation in PRI among fluorescence parameters was described by changes in non-photochemical quenching (Fig. 5 in **II**, Table 5 in **II**). It is probable that treatments influenced the carotenoid/chorophyll relationship of plants, which has been shown to be another parameter that affects the PRI signal (Filella et al. 2009). However, as the relationships between PRI and plant physiological traits appear to be species-specific, much work remains to be done to understand the

short and long-term factors influencing the values of PRI for different plant communities (Peñuelas et al. 1995, Ahl et al. 2004, Filella et al. 2004, Liu et al. 2013).

3.4. Effect of canopy structure on light use efficiency of canopies and single leaves

Our results in European shrublands showed that the structure of vegetation (approximated as the variation in green LAI_e) clearly explained the largest part of the variation in the reflectance index PRI (Table 5 in **II**), even if PRI was significantly related to the physiological traits of vegetation. In fact, it is shown that not only LAI but also the vertical structure of the canopy and leaf orientation affects values of PRI (Nichol et al. 2000, Barton and North 2001, Damm et al. 2010). Barton and North (2001) demonstrated that angle between leaf normal and the sun determines the intensity of light received by the leaf and hence the LUE and PRI of the leaf, but also it determines the signal strength from that leaf and therefore its relative contribution to canopy PRI. Thus, as real canopies vary in leaf angle distributions, and this changes during plant growth and due to changes in environmental conditions, it is very problematic to draw a single function which transfers PRI or fluorescence yield into LUE of the whole canopy without considering differences in canopy structure (Barton and North 2001, Damm et al. 2010). In the case of forests the effect of structure and resultant leaf-level light-acclimation differences on parameters of remote sensing are even more severe, as the fraction of leaves of the whole canopy that can actually be remotely "sensed" from a single view angle is even smaller. Fortunately the first steps for incorporating estimations of shadow fraction into remote estimations of LUE have recently been taken (Hall et al. 2011, 2012, Hilker et al. 2012) and an increasing network of carbon dioxide flux measurement towers (Baldocchi, 2008) further helps us to understand the deviations between remotely sensed vegetation indices and carbon fluxes of whole communities.

In **III** we focused on the impact of canopy structure on light capture efficiency of forest ecosystems, more specifically on leaf- and chloroplast-level light acclimation differences between two contrasting tree species. An often used equivalent for leaf-level light use efficiency is quantum capture efficiency of a leaf, estimated by changes in fluorescence emission. Differences in quantum efficiencies of leaves have often been demonstrated along the vertical light gradient of the forest canopy (Fig. 1 d–f in **III**). Less noticed is the within-leaf chloroplast acclimation profile, which also adapts to changes in light environment. In fact, similarly to other optical methods, leaf-level fluorescence measurements also estimate light capture efficiency remotely, and our aim was to evaluate the dependence of fluorescence-based light capture efficiency estimations on canopy structure, focusing on leaf angle distribution (**III**).

Our measurements of chlorophyll fluorescence in trees showed that the ratio of Φ_{II}, qP and NPQ between alternate leaf sides, as an approximation of intra-leaf light acclimation differences, significantly correlated with leaf angles (Fig.

3 in **III**). The ratio between quantum use efficiency of alternate leaf sides was in general larger in more horizontal leaves, as opposed to vertically oriented leaves. However, our results also indicated that the relationship between adaxial/abaxial quantum use efficiency of leaves and leaf angles was species specific (Fig. 3 in **III**), being significant in the case of light-demanding *Populus tremula* and not significant in shade-tolerant *Tilia cordata*. Considering that the chlorophyll fluorescence of only the upper side of the leaf is often used for estimating the light capture efficiency of the whole leaf, our results indicate that, depending on species, the actual light capture efficiency of the whole leaf can be a function of local light conditions that are determined by leaf angle.

Tsuyama et al. (2003) suggested that the measurements of gas exchange and chlorophyll fluorescence detect signals from different populations of chloroplasts in a leaf. If so, the disproportion between fluorescence measurements of leaf abaxial side and gas exchange measurements might also be different for leaves with different orientation and resultant light conditions. This is because variations in the light conditions of different subpopulations of chloroplasts can change the correlation between whole-leaf photosynthetic properties and the photosynthetic properties of individual chloroplasts near the leaf surface, from where the fluorescence signal is mainly derived (Peguero-Pina et al. 2009). At the same time the region from which the fluorescence signal originated also depends on leaf structure, chlorophyll content and excitation wavelength (Cui et al. 1991, Evans 1999, Vogelmann and Han 2000, Buschmann 2007, Peguero-Pina et al. 2009), all of which change depending on leaf orientation and species. Therefore, for parameterization of vegetation structure so that leaf-scale properties may be related to the properties of the whole ecosystem, different adaptation strategies of species must be taken into account. Unfortunately only a few models currently include representations of specific plant responses, probably because available empirical studies are often not at scales relevant for models (Smith and Dukes 2013).

3.5. Chlorophyll distribution within leaves and canopy

Although leaf angles correlated with the gradient of within-leaf physiology, leaf orientation is merely controlling the amount of photochemically active radiation that is received by both leaf sides at different depths in the forest canopy. Thus, to understand the mechanisms behind the above discussed differences in leaf light use efficiency and optical estimations of light use efficiency, we performed additional studies. In **III** and **IV** we investigated the physiological traits that respond to differences in local light environment and thus produce the different fluorescence figures for alternate leaf sides. First we studied leaf reflectance in red and green spectral regions, which, similarly to fluorescence signals are influenced by a combination of leaf anatomy and biochemistry (Govaerts et al. 1996, Peguero-Pina et al. 2009). Leaf reflectance and absorptance measurements from alternate leaf sides indicated that light demanding *P.*

tremula enhanced the photosynthetic potential of leaf biochemistry by decreasing the interception of excess irradiance on the abaxial side of the leaf by increased reflectance (Table 1 in **III**), resulting in smaller differences in fluorescence parameters measured from leaf adaxial and abaxial surfaces (Fig. 3 in **III**). Shade-tolerant *T. cordata* on the other hand increased the light absorptance of leaves (Table 1 in **III**).

Based on earlier studies, which have determined leaf-area-based chlorophyll content (Chl_s) and leaf mass per area (LMA) as being the best proxies for light adaption of the photosynthetic apparatus of leaves (Tsuyama et al. 2003), we investigated Chl_s and LMA as parameters correlating to most of the optical and photochemical differences between alternate leaf sides. Indeed, LMA and chlorophyll content correlated with optical properties for a single species (Fig. 4 in **III**). But when we pooled together data from both species with different strategies (shade-tolerant and light-demanding) the correlative relationship often failed (Fig. 4 in **III**). Furthermore, leaf reflectance and absorptance in the green spectral region were more strongly correlated to variations in leaf chlorophyll content and LMA than reflectance and absorptance measured from the strongly absorbing red spectral region (Table 2 in **III**). Within one species, LMA explained more of the variance in leaf optics than Chl_s (Table 2 in **III**), possibly because the arrangement of chloroplasts can be a more important determinator of light capture than the quantity of chlorophyll *per se* (Souza and Válio 2003).

The importance of leaf structural properties in regulating light use efficiency became especially evident with the finding that *P. tremula* with leaves of significantly more mass per area than *T. cordata* (Fig. 1b in **III**), revealed lower values of absorption (Table 1 in **III**) and smaller differences between light dissipation regulations of alternate leaf sides (NPQ, Fig. 3 in **III**). However, for light-demanding *P. tremula*, leaf angles appeared to be better estimators of differences between quantum use efficiency of alternate leaf sides (Fig. 3 in **III**) than LMA or Chl_s, contrary to *T. cordata*, where the ratio of adaxial/abaxial NPQ was significantly correlated to LMA (r=0.52, p<0.05). The results given in **IV** confirmed our findings of species specific differences in chlorophyll distribution, as similar shade adjustment of LMA was accompanied with modest changes in chlorophyll concentration, while the densities of different photosynthetic units adjusted to light differences more extensively (Table 1 in **IV**).

In order to investigate more precisely the rearrangement of pigments and to find which parts of the photosynthetic machinery are most responsive to differences in light conditions, we performed an additional investigation (**IV**). Main chloroplast parameters, which have shown to influence the efficiency of light harvesting in photosystem II are the number of LHCII subunits, the arrangement of pigments within them, the interaction between subunits and their distance from the reaction centre complex (Horton 2012). Our results on chlorophyll a/b ratio (Chl a/b) showed significant redistribution of chlorophylls due to acclimation to shade in the canopies of the measured tree species (Fig. 3). The parameter Chl a/b is often used as a measure of the distribution of chlorophyll between antenna and core complexes of the photosynthetic machinery, as most

studies show that Chl b is present mainly in the antenna complex of photosystem II (LHCII) (Evans 1989, Green & Durnford 1996, Kitajima and Hogan 2003). However, recent studies have shown significant migration of LHCII to PSI complexes during state transition (Minagawa 2011) and in mutant plants lacking state transitions, LHCI itself can be enriched in chlorophyll b (Ruban et al. 2003, Ruban and Johnson 2009). Thus it may be difficult to deduce the actual quantity of LHCII of PSII complex from the changes in Chl a/b in natural canopies.
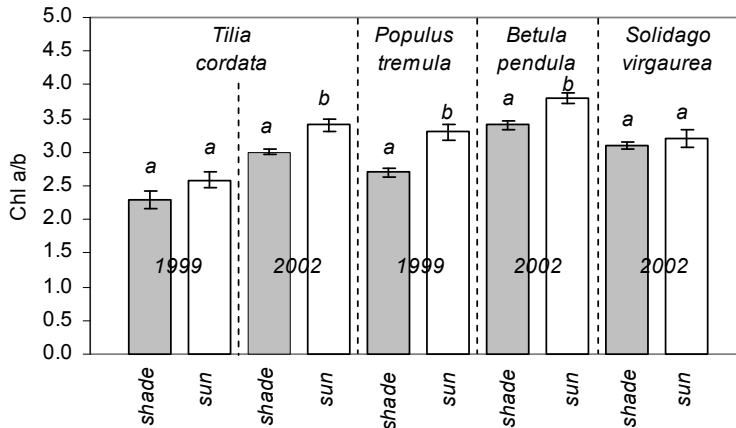
Figure 3. Ratio of leaf chlorophyll a and b for different deciduous forest species, measured in different study years. Different letters at the top of columns indicate significant differences between shade and sun leaves of the same species and same year according to Wilcoxon signed rank test, p<0.001.

Our calculations of realistic shade acclimation in natural forest systems (**IV**) showed that sun leaves of *B. pendula* on average attached 2.2 trimers of LHCII to PSII, while shade leaves of the same species on average added one more trimer of LHCII to the PSII core, resulting in 3.2 LHCII trimers per PSII on average at shade. The addition of one trimer of LHCII was accompanied by a decrease in Chl a/b ratio of *B. pendula* by 0.4 units in shade, which is consistent with earlier studies (Walters et al. 1999). At the same time the similar decrease of 0.4 units of Chl a/b in the shade-adapted leaves of *T. cordata* did not mean a similar increase in LHCII per PSII. In sun leaves of *T. cordata*, on average 2.6, and in those of *Solidago virgaurea*, 3.9 LHCII trimers were attached to PSII, but the average number of trimers did not change due to shade adjustment in those two species (Table 1 in **IV**).

According to our data, the main difference between *B. pendula* and *T. cordata* lied in different densities of PSI and PSII and in the size of PSI antenna (Table 1 in **IV**). The light adjustment of LHCII is widely known, but our results indicate significantly larger light adjustment of PSI, which increased by about

two LHC trimers due to shade adjustment in *Betula pendula* and was larger on average than the PSII antenna of same leaves (Table 1 in **IV**). A similar doubling of the light harvesting complex of PSI has been observed by Bailey et al. (2001), while Ballottari et al. (2007) recorded no adjustment of numbers of LHCI in *Arabidopsis thaliana* and revealed that the increase in light capture ability of PSI at low light conditions was achieved through migration of LHCII to PSI complex. It is most probable that the increase in PSI LHC due to shade adjustment in **IV** was also caused by the migration of two trimers of LHCII to PSI. Recently a lot of work has been done in order to understand the environmental triggers for the photosynthetic state transitions and accompanying migration of LHCII to PSI-LHCI systems (Kovács et al. 2006, Ruban and Johnson 2009, Minagawa 2011, Kouřil et al. 2013), but a lot more needs to be done to understand this mechanism at the level needed for ecological applications. Most probably the capacity for state transitions might be one of the parameters determining the light use efficiency of different species.

Our investigations showed that an increase in PSI antenna occurred not due to increasing chlorophyll concentration, but due to decreasing PSI density in all studied species (Table 1 in **IV**) and therefore an increasing PSII/PSI ratio with decreasing irradiation was found in all studied species. Most probably the decreasing density of PSI with shade can be associated with a higher proportion of far-red irradiation, which has been shown to be characteristic of lower layers of the forest canopy (Lieffers et al. 1999), since previous studies have shown that changes in red/far-red ratio of irradiation may cause changes in photosystem stoichiometry (Chow et al. 1990, Murchie and Horton 1998). A paper by Ruban et al. (2006) showed that the LHCI antenna itself can also be considerably upregulated when state transition is absent, however no data exists on wild-type species with the absence of photosynthetic state transition. Several contradictions in papers on light acclimation of photosystems suggest that the acclimational changes of PSI might be species specific, and thus, studies on single model-species cannot be applied to a larger set of species. Very little is yet known also about the effect of spectral differences at the top and bottom of forest canopies on the differences in the photosystem composition and how this relates to the quantum yield of photosynthesis (Hogewoning et al. 2012). Our findings of different stoichiometrical changes in chlorophyll distribution between different species as a result of shade explain the reports of species specific relationship between PRI and plant physiology (Peñuelas et al. 1995, Ahl et al. 2004, Filella et al. 2004, Liu et al. 2013) as canopy reflectance measurements often reflect more strongly certain aspects of light use efficiency, such as PRI is significantly influenced by the xanthophyll cycle of nonphotochemical quenching, underestimating the possibility that similar light use efficiency may be achieved through alternative mechanisms of light capture and re-funnelling of excess light.

3.6. Nitrogen distribution within leaves and canopy

The high density of chlorophyll in light harvesting complexes is crucial for efficient use of leaf nitrogen as nitrogen availability is often limiting photosynthesis. Remarkably small concentration of nitrogen-containing proteins binds chlorophylls in light harvesting complexes in a way, which enables the efficient capture of light (Beddard and Porter 1976). Despite of nitrogen-efficient molecules of light capture plants appear to optimize nitrogen use at every step of light acclimation. Besides modest changes in chlorophyll concentration, we found concentrations of leaf nitrogen and the nitrogen-rich protein ribulose-bisphosphate carboxylase-oxygenase (Rubisco) per leaf area to be more responsive to changes in light conditions, as nitrogen of leaves decreased by a factor of three and Rubisco decreased by a factor of four as a response to shade if measured on the basis of leaf area (Fig. 7 in **IV**). Fig. 4 shows that a similar decrease in leaf-area-based nitrogen (N_s) was present both in the vertical light gradient of the forest canopy of **III** and in the case of decreasing annual irradiance associated with the vertical distance between different shrublands in Europe (**I** and **II**). However, the significant shade acclimation for nitrogen and protein concentration came mainly from differences in LMA, since mass-based leaf nitrogen (N_m) was not significantly related to different light regimes.
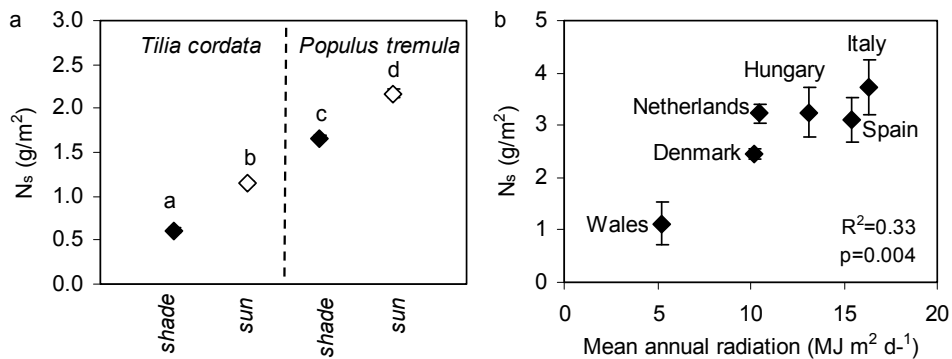
Figure 4. Leaf-area-based nitrogen content of (a) lower canopy species *T. cordata* and upper canopy species *P. tremula* in a deciduous forest in Järvselja, Estonia and (b) dominant species of six European shrublands. Mean±St. Err. are shown, different letters on top of mean values of forest species denote significant differences between sites according to Fisher LSD post-hoc test.

According to our results on forest species with similar nitrogen availability, N_s investment into light-harvesting components of photosynthesis increased as a result of shade acclimation, while N_s invested into Rubisco decreased (Fig. 8 in **IV**). Our results indicated that the larger investment of nitrogen into light-harvesting proteins in shade might not be enough to keep the excitation rate of a

PSII centre invariant. As PSI is in close contact with the carbon assimilation system, the density of PSI shade-adjusted almost proportionally to changes in Rubisco, while antenna of PSI correspondingly increased (Fig. 8 in **IV**). The general changes in Rubisco and light capture compartments did not differ considerably between the herbaceous species *Solidago virgaurea* and tree species (Fig. 7 in **IV**), in contrast to what was theoretically predicted by a nitrogen allocation model by Xu et al. (2012). The model (Xu et al. 2012) predicted that lower levels of radiation will have a much stronger effect on the allocation of nitrogen to carboxylation for herbaceous plants than for trees, based on the assumption of proportionally smaller investment of nitrogen into the cell walls of herbaceous leaves. However, the non-photosynthetical nitrogen is not just in cell-walls but also in amino acids, nucleic acids, cytosolic proteins, ribosomes and mitochondria (Evans and Seemann 1989, Hirose et al. 1989). Additionally it has been shown that part of the Rubisco can be inactive and is functioning as reserve protein (Eichelmann and Laisk 1999, Warren et al. 2000).

Our study, on the other hand, excluded also the inactive Rubisco from the calculations of non-photosynthetic nitrogen. Nevertheless, we found that leaf acclimation to shade was followed by a considerable decrease in the reserve of non-photosynthetic fraction of nitrogen (Fig. 7 in **IV**) in tree species and also in the herbaceous *Solidago virgaurea*. Recently the effect of variation in the non-photosynthetic component of N on nitrogen allocation to photosynthesis has been further investigated and it was found that nitrogen investment to cell walls does not always affect the content of photosynthetic N (Hikosaka and Shigeno 2009) although N in cell walls is strongly related with LMA as was expected previously (Hikosaka 2004). However, as the non-photosynthetic N fraction does change within a single canopy, extrapolation of nonphotosynthetic N content from the nitrogen-photosynthesis relationship, where photosynthesis has reached zero, might be questionable (Wright et al. 2004).

Thus investigations on a larger variety of species are needed to understand the origin and variability of the non-photosynthetic fraction of nitrogen in different functional groups, since our study indicated the importance of light acclimation of non-photosynthetic N also in short-lived herbaceous species. Similarly the variability in Rubisco has not yet been studied across a range of different species, although there are indications that the relationship between leaf maximum carboxylation capacity and leaf-area-based photosynthetic nitrogen differ between plant functional groups (Maire et al. 2012). Significant differences in the light-acclimation related variability in photosynthetic compartments or non-photosynthetic N may have considerable effect on modelling vegetation production using C/N relations. This might become even more relevant, if canopy nitrogen content is aquired from remotely sensed data that does not consider within-canopy variation in the fraction of non-photosynthetic nitrogen in leaves.

3.7. Nitrogen budget in relation with carbon production of vegetation

The availability of nitrogen has been shown to be one of the main constraints in the carbon cycling of terrestrial ecosystems (LeBauer and Treseder 2008), and models of ecosystem functioning need input info about nitrogen pools and fluxes of different ecosystems. Nevertheless, very fragmented data is available on the nitrogen cycle of shrublands. Thus in **I** we constructed an integrated scheme of aboveground and belowground nitrogen distribution and fluxes at six European shrubland ecosystems (Fig. 7 in **I**). The largest nitrogen resources (468 g N m^{-2}) were found in soil organic matter and roots of the wettest and coldest shrubland in the UK, while lowest values of belowground nitrogen (93 g N m^{-2}) were found on Hungarian dry and sandy soils (Fig. 7 in **I**) however, the ratio of C/N in the top soil was also largest at the UK site and lowest at the Spanish site (Table 2 in **I**). We found that the size of the aboveground nitrogen pool of the studied shrublands was 2–6% of the belowground nitrogen concentration (Fig. 7 in **I**).

On the other hand, the aboveground nitrogen content, measured as average nitrogen content per leaf area generally increased with increasing light availability according to our study (Fig. 4), and nitrogen has been shown to relate significantly also with photosynthesis across various species and vegetation types (Reich et al. 1997, Niinemets et al. 2001, Green 2003, Niinemets 2010). Therefore, relationships between canopy irradiance, nitrogen and photosynthesis are used for modelling global carbon exchange between vegetation and the atmosphere (Friend 2001, Mäkelä et al. 2008), but these known relationships are mainly scaled up from leaf-level measurements. Recently also a strong relationship between remotely sensed nitrogen content of aboveground vegetation and photosynthetic capacity of whole canopy has been reported for forest ecosystems (Ollinger et al. 2008). However, Ollinger et al. (2008) did not include respiration into their calculations and thus they were not able to conclude, whether changes in nitrogen content and photosynthesis will always lead to a variation in net carbon sequestration. Also the prediction of carbon sequestration using data on canopy nitrogen content may be problematic in changing climate conditions, as a review paper by Sardans et al. (2012) showed significant differences in C/N relationships of plants as a response to changed climate and nitrogen deposition.

Nevertheless, our results on six shrublands suggested that canopy nitrogen content of shrublands possibly gives information about the most variable component of primary production, the light use efficiency (LUE), since an index of LUE, which was calculated as a function of leaf nitrogen content (see equation 20. of thesis; Green et al. 2003), was significantly correlated with calculations of LUE and remotely sensed PRI (Fig. 2). For a large variety of forest tree species, maximal light use efficiency has also been found to depend linearly on nitrogen content (Kergoat et al. 2008, Peltoniemi et al. 2012) at all levels of incident PPFD, while Peltoniemi et al. (2012) found that canopy LUE increased at all forest sites by 23% when mean canopy N increased from 1 % to 2%.
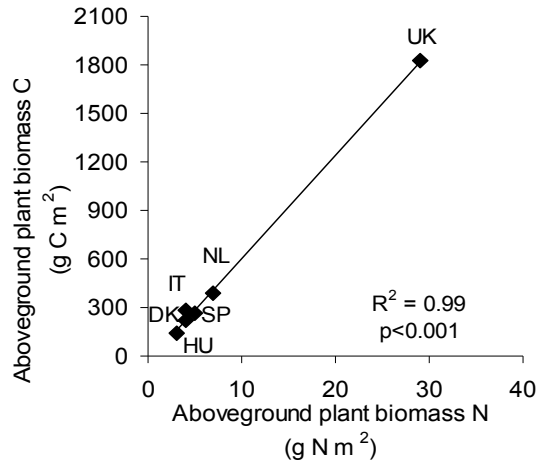
Figure 5. Relationship between mean carbon and nitrogen content of six European shrubland ecosystems.

According to six shrublands of present study, the aboveground nitrogen content and aboveground carbon pools appeared to be linearly related (Fig. 5), suggesting that using nitrogen content of vegetation for estimating vegetation productivity could be valid also for European shrublands. However, for more conclusive results additional data on shrublands with medium to high biomass would be needed. Also, further investigations on the same shrublands by Beier et al. (2008) revealed that C and N cycles respond asymmetrically to warming treatment and concluded that global warming effects on shrublands may lead to progressive nitrogen limitation and resultant changes in plant production. As the effect of climate on C/N relationships in plants is shown to be quite universal (Sardans et al. 2012), estimations of carbon sequestration using data on canopy nitrogen content is even more complicated. On a global scale the inevitable factor determining the C/N ratio of the vegetation is the proportion of wood in plants (Wania et al. 2012). We found the average C/N ratio to be 68 in European shrublands (carbon/nitrogen in aboveground plant parts and roots), which is consistent with that predicted for shrubs by a model of Wania et al. (2012), predicting an average C/N for shrublands to be 75±37. However, at large scale there is a discrepancy between calculations of global C/N ratio, since very different estimations of global nitrogen concentrations (3–18 Pg N) have been reported for the same years (Lin et al. 2000, Yang et al. 2009, Zaehle et al. 2010, Wania et al. 2012), resulting in average global C/N ratio to vary extensively from 30–200 (Wania et al. 2012). Thus the relationships between canopy-scale nitrogen concentration and plant production still need to be tested in different ecosystem types and climatic conditions on a canopy scale, and information on the nonphotosynthetic proportion of canopy and root N is evidently lacking.

4. CONCLUSIONS

1. We conclude that in remote estimations of carbon budget of shrublands, considerable accumulation of carbon into belowground must be taken into account. In case of studied shrublands the average ratio of belowground/litterfall carbon content in general exceeded the respective ratio of carbon reported for forest systems. Nevertheless, the sizes of above- and belowground carbon pools of different shrublands were related to each-other. European shrublands ranged from being carbon sinks to carbon sources and differed in soil nitrogen content and availability.

2. Differences in green leaf area index and light use efficiency of vegetation were efficiently detected by remotely measured canopy reflectance indexes NDVI and PRI above several European shrublands. However, the relationship between NDVI and green leaf area index tended to saturate at dense shrublands, even if the green spectral region was used in NDVI calculations instead of red. Nevertheless, in dense northern shrublands the relationship was found to be stronger if NDVI was calculated using the green spectral region. Reflectance index PRI appeared to be closely related to changes in light use efficiency of plants at dense northern shrublands, but this relationship was absent in sparse southern shrublands. The treatment effects on green leaf area index and light use efficiency, estimated by reflectance indexes, were minimal and differed in directions of change between shrublands.

3. This study revealed strong effect of canopy structure on the canopy- and leaf-level estimations of light use efficiency. The reflectance parameter PRI was significantly influenced by variations in green leaf area index of shrublands. Measurements of leaf fluorescence revealed, that for light-demanding *Populus tremula*, leaf angles appeared to estimate the differences between light use efficiency of alternate leaf sides (suggesting within-leaf differences in chloroplast acclimation to light), compared to *Tilia cordata*, where the differences in chloroplast light acclimation were better correlated to leaf mass per area.

4. Our investigations of within-leaf mechanisms that influence leaf light use efficiency revealed that differences in leaf chlorophyll a/b ratios, which have long been used as a proxy for chlorophyll distribution between light harvesting complex of photosystem II and core complexes of photosystems, reflected different stoichiometrical changes in different species. Unlike many earlier studies, we found that the size of light harvesting complex of photosystem I and the abundance of photosystem I were more responsive to differences in irradiance than the size of light harvesting complex of photosystem II.

5. We demonstrated that the main leaf trait changing due to light adjustment in all studied species appeared to be the non-photosynthetical fraction of leaf nitro-

gen, variation of which may have significant effect on modelling vegetation production using C/N relation and remotely sensed nitrogen estimations.

6. The finding of significant correlation between light use efficiency and nitrogen based index of light use efficiency according to six shrublands suggests that at European shrublands it may be possible to calculate canopy light use efficiency as a function of canopy nitrogen, since the aboveground nitrogen and carbon pools of studied shrublands were also related, however reports of significant changes in carbon/nitrogen ratios of plant tissues as a result of changing climate may complicate the extrapolation over larger areas and over time.

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SUMMARY IN ESTONIAN

Taimede valguskasutuse efektiivsus ning süsiniku ja lämmastiku bilanss: kaugseire kasutamine ja füsioloogilised determinandid

Globaalse kliima pidev muutumine põhjustab muutusi maailma erinevate taime-koosluste primaarproduktsioonis, mistõttu uuritakse järjest enam taimkatte sü-sinikuringet mõjutavaid tegureid. Selleks, et me võiksime piisava täpsusega en-nustada muutusi süsiniku sidumises ja primaarproduktsioonis, on vaja teada, mil moel keskkonna erinevad omadused primaarproduktsiooni mõjutavad.

Laias laastus määrab taimkatte produktsiooni taimede eri osadeni jõudev fotosünteetiliselt aktiivse kiirguse hulk ning valguse kasutamise efektiivsus tai-mede fotosünteesisüsteemi poolt. Neid kahte primaarproduktsiooni osa mõjuta-vad omakorda erinevad tegurid, teiste hulgas võra ja lehe liigi- ja kooslusespet-siifiline ehitus, fotosünteesiaparaadi võime kohaneda valgustingimuste erine-vustega, mullalämmastiku kättesaadavus ning lämmastiku kasutamise tõhusus, vee kättesaadavus ja temperatuur. Arvestades ülemaailmsete uuringute ulatust, ei ole võimalik muutusi taimede süsinikutasakaalus jälgida vaid paikkondlikult - väga oluline osa taimede ökofüsioloogilistest uuringutest baseerub kaugseire-infol. Seetõttu on kaugseire abil saadud taimkatte peegeldumisindeksite täiusta-mine ja kasutatavuse hindamine erinevates taimekooslustes üks olulisemaid tai-mede ökofüsioloogia uurimissuundi tänasel päeval. Et aga kindlaks teha taim-katte peegeldumisindekseid mõjutavad tegurid, on jätkuvalt oluline mõista, mil viisil toimub erinevatele taimeliikidele ja funktsionaalsetele gruppidele omane valguskohanemine nii võra, lehe kui ka kloroplasti tasandil. Seejuures on kloro-plasti tasandil toimuva valguskohanemise mehhanismide varieeruvuse kohta reaalsetes taimekooslustes vähe infot. Sama oluline on uurida lehe valguskasu-tuse tõhusust mõõtvate tulemuste laiendatavust kogu võrale ja kooslusele, kuna taimevõra valguskasutuse efektiivsuse n-ö alt üles modelleerimisel võib võra struktuurierinevuste või kloroplasti tasandil toimuvate erinevate valguskohane-mise strateegiatega arvestamine oluliselt parandada mudeli vastavust reaalsu-sega.

Käesoleva doktoritöö laiemaks eesmärgiks oli uurida, millised faktorid mõjutavad taimkatte produktsiooni ja selle hindamist kaugseire meetodeil, kes-kendudes valguskasutuse efektiivsusele, mis on primaarproduktsiooni üks va-rieeruvamaid ja raskemini ennustatavaid komponente. Uuriti, millised taimede parameetrid reageerivad kõige ulatuslikumalt muutustele valguskeskkonnas ning kuidas nende parameetrite erinevad väärtused mõjutavad taimkatte valgus-kasutuse mõõtmisi nii lehe kui võra tasandil.

Töö kitsamad eesmärgid olid järgmised.

1. Kaardistada taimede süsiniku- ja lämmastikuvarusid erinevates Euroopa puhmastikukooslustes.

2. Analüüsida kaugseire meetodil mõõdetud peegeldumisindeksite NDVI ja PRI kasutatavust Euroopa puhmastike primaarproduktsiooni komponentide - efektiivse lehepinnaindeksi (green LAI_e) ja valguskasutuse efektiivsuse (LUE) - hindamisel.
3. Uurida võra ja lehestiku struktuuri mõju valguse kasutamise efektiivsuse mõõtmistele.
4. Uurida, kuivõrd varieerub liigiti ja võra erinevates piirkondades klorofülli jaotus lehes, mis omakorda mõjutab taimede valguse kasutamise efektiivsust.
5. Uurida looduslikku varieeruvust fotosünteetilise ja mittefotosünteetilise lämmastiku hulgas ning jaotuses erinevatel liikidel ja erinevates valgustingimustes.
6. Uurida Euroopa puhmastike näitel, kas taimede lämmastikusisalduse alusel on võimalik kaudselt hinnata süsinikuproduktsiooni.

Loetletud eesmärkide saavutamiseks viidi läbi kaks erinevat eksperimenti. Uuriti koosluse süsiniku ja lämmastiku jaotust ning hinnati kaugseire meetodeid kuues erineva valgus-, niiskus- ja temperatuurirežiimiga puhmastikus: Suurbritannias Walesis, Taanis, Hollandis, Ungaris, Hispaanias Kataloonias ja Itaalias Sardiinias. Lisaks pidevale keskkonnaparameetrite salvestamisele mõõdeti ka taimede ja varise süsiniku ning lämmastiku kontsentratsiooni, mulla lämmastikuühendite ja lahustunud orgaaniliste ühendite sisaldust, taimkatte struktuuri parameetreid, mulla hingamist ja dominantsete liikide ülemistel lehtedel klorofülli fluorestsentsi. Lisaks mõõdeti 1 m kõrguselt taimkatte kohalt peegeldumisindeksid NDVI (spektri punasest piirkonnast $NDVI_{680}$ ja rohelisest piirkonnast $NDVI_{570}$) ja PRI.

Valguskasutuse efektiivsuse ja seda mõjutavate faktorite, klorofülli ja lämmastiku jaotumise varieeruvust lehes, võras ja liigiti uuriti Eestis Järvselja heitlehises segametsas, kus võrastiku tornid lubasid ligipääsu erinevate valgustingimustega kohanenud lehtedele. Lehe eri külgedelt mõõdeti erinevates valgustingimustes kasvanud lehtede klorofülli fluorestsentsi ja peegeldumist spektri nähtavas osas ning hinnati lehe ja erinevate fotosünteesisüsteemi komponentide klorofülli- ja lämmastikusisaldust.

Selleks, et kaugseire meetodeil hinnata muutusi puhmastike primaarproduktsioonis, on vaja infot süsiniku jaotumise ja biokeemiliste tsüklite kohta puhmastikukooslustes, kuna erinevalt metsa- ja niidukooslustest on süsiniku ja lämmastiku tasakaalu puhmastikes üsna vähe uuritud. Käesoleva uurimuse tulemusel selgus, et Euroopa puhmastikud varieeruvad oluliselt süsiniku omastamise poolest. Uuritud puhmastike hulgas leidus nii süsinikku neelavaid kooslusi (126 g C m^{-2} a^{-1} niiskes Walesi kanarbiku-mustikapuhmastikus) kui ka süsiniku emiteerijaid (-536 g C m^{-2} a^{-1} mittestabiilses kuivas Itaalia puhmastikus). Niiskes Walesi puhmastikus oli samuti suurim mulla lämmastikusisaldus (468 g N m^{-2}), madalaim oli see aga Ungaris kuival liivmullal (93 g N m^{-2}). Vaatamata kõrgele süsiniku sidumisele ja mulla lämmastikusisaldusele, oli lämmastiku kättesaadavus üheks taimede kasvu pidurdavaks teguriks Walesi puhmastikus: mulla C/N suhe

Walesi puhmastikus oli 37,4, samas kui vastav suhe kuivas Hispaania puhmastiku mullas oli 12,8. Maapealsete taimeosade süsinikusisaldust puhmastikes mõjutas tugevalt keskkonna niiskusrežiim. Kuigi niiskusrežiimi mõju maa-alusele süsinikusisaldusele ei väljendunud nii selgelt, olid maapealne ja maa-alune süsinikusisaldus omavahel tugevas mittelineaarses seoses. Tänu maapealse ja maa-aluse süsiniku kontsentratsioonide tugevale seotusele on põhjust otsida võimalusi ka kogu koosluse primaarproduktsiooni hindamiseks puhmastikukoosluste kohalt kaugseire meetodite abil.

Varasemalt on näidatud, et kaugseire meetodeil saadud peegeldumisindeks NDVI väärtused sõltuvad taimkatte efektiivse lehepinnaindeksi (green LAI$_e$) väärtustest ja taimede poolt neelatud fotosünteetiliselt aktiivse valguse hulgast. Käesolev uurimus näitas, et NDVI väärtused olid küll oluliselt seotud muutustega puhmastikukoosluste efektiivses lehepinnas, kuid NDVI väärtused küllastusid keskmiste ja suuremate green LAI$_e$ väärtuste juures isegi juhul, kui indeksi arvutamisel kasutati spektri rohelist piirkonda (570 nm) punase (680 nm) asemel. Siiski oli tihedates põhjapoolsetes puhmastikes NDVI ja green LAI$_e$ vaheline seos tugevam juhul, kui NDVI arvutamisel kasutati spektri rohelise piirkonna väärtusi. Teise peegeldumisindeksi, PRI väärtusi kasutatakse taimekoosluste valguskasutuse efektiivsuse hindamiseks. Käesoleva uuringu põhjal korreleerusid erinevate puhmastike PRI väärtused taimede lämmastikusisalduse baasil arvutatud valguskasutusefektiivsuse indeksiga. Samuti oli PRI tihedates põhjapoolsetes puhmastikes tugevalt seotud taimelehtede kohalt mõõdetud valguskasutuse efektiivsuse väärtustega, kuid lõunapoolsetes puhmastikes taoline seos puudus. Kui uurisime kunstlikult tekitatud põua ja öise temperatuuri tõusu mõju puhmastikele, siis põua tõttu puhmastike NDVI keskmised väärtused enamasti vähenesid ja temperatuuri tõustes PRI väärtused enamasti suurenesid, kuid üksikute puhmastike lõikes oli mõõduka temperatuuritõusu ja põua mõju produktsiooni erinevatele komponentidele vähene ja eri maades isesuguse suunaga.

Nii puhmastikukooslustes kui ka Järvselja metsas toimunud uuringud näitasid, et taimede ja koosluse struktuur mõjutab tugevalt nii lehtede (fluorestsentsi mõõtmised) kui koosluse (PRI mõõtmised) valguskasutamise efektiivsuse mõõtmisi. Peegeldumisparameeter PRI näitas valguskasutuse efektiivsust tunduvalt halvemini hõredamates puhmastikes, kus PRI väärtusi mõjutas heleda mulla peegeldumine taimestiku vahelt. Lehe tasandil toimunud mõõtmised näitasid, et ülemise metsarinde liigi, hariliku haava (*Populus tremula*) puhul oli erinevuste järgi lehe nurkades võimalik hinnata lehe üla- ja aläküljelt mõõdetud valguskasutuse efektiivsuste erinevusi (Φ_{II} lehe ülakülg / Φ_{II} lehe alakülg), mis omakorda viitab nähtusele, et erinevused lehe nurkades peegeldavad erinevusi lehtede kloroplastide valguskohanemises. Metsa alumise rinde puuliigi, hariliku pärna (*Tilia cordata*) puhul aga kajastasid lehtede pindtiheduse (LMA) erinevused muutusi lehe eri külgedelt mõõdetud liigse valguse eemale juhtimises (NPQ lehe ülakülg / NPQ lehe alakülg) paremini kui lehe nurgad. Lehe eri külgede teistsugune valguse kasutamine tingib selle, et erinevate nurkade ja pindtihedustega lehtede puhul kirjeldavad fluorestsentsi meetodil lehe ülaküljelt

mõõdetud valguskasutuse efektiivsuse väärtused erinevat fraktsiooni lehe kloro-plastidest.

Uurides seejärel põhjalikumalt taimede valguskohanemise mehhanisme, selgus, et kloroplastide valguskohanemise tulemusena muutub lehes klorofüll a ja b jaotus. Metsa ülarinde liigi, arukase (*Betula pendula*) varjulehtedes lisandus fotosüsteem II (PSII) valguspüügi süsteemile (LHC) üks täiendav trimeer ja fotosüsteem I (PSI) valguspüügi aparaadile lisandus varjus kaks trimeeri. Hariliku pärna või hariliku kuldvitsa (*Solidago virgaurea*) puhul sellist selget LHC suurenemist ei ilmnenud. Küll aga vähenes kõigil uuritud liikidel PSI tihedus lehes, mistõttu kõigi liikide varjulehtedes suurenes PSII/PSI suhe. Lehe lämmastikusisaldust mõjutasid veelgi enam erinevused valgustingimustes. Varjulehtedes suurenes sellise lämmastiku hulk, mis oli paigutatud LHC-sse, ning vähem lämmastikku paigutati Rubisco ning PSI tootmisesse. Eriti rõhutas käesolev uuring mittefotosünteetilise lämmastiku osalust taimede valgusega kohanemises, kuna tulemused näitasid, et erinevates valgustingimustes varieerus kõige enam mittefotosünteetilise lämmastiku kogus. Taimede lämmastikusisalduse tugevat seotust valguse kasutamisega näitas ka koosluse valguse kasutuse efektiivsuse (LUE) hea korrelatsioon lehtede lämmastikusisalduse baasil arvutatud LUE-indeksiga, kusjuures erinevate Euroopa puhmastike maapealsed lämmastiku- ja süsinikuvarud olid omavahel seotud.

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- Coordinating the building of of websites advertizing the research topics of department of Botany, preparing website of plant ecophysiology and organizing a seminar introducing the research topics of department of Botany for bachelor students, 2007
- Organizing a weekly seminar "Journal club" for graduate-students of biology at 2006/2007
- Member of organizing team of international doctoral school of NordForsk and Doctoral School of Earth Sciences and Ecology, Estonia: Tree canopy – structure and functioning – from below and above. 3–14 September 2006, Järvselja and Vihula, Estonia
- Member of organizing team of spring-schools of "Theorethical Biology" at years 2004–2006
- Member of Estonian Naturalists Society
- Member of Estonian Seminatural Community Conservation Association
- Member of Tartu Students' Nature Protection Circle (1998–1999 in board)

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> Tartu Ülikool, *BSc* bioloogia erialal (2000)
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Keelteoskus: eesti, inglise, vene, saksa

Teenistuskäik:
2003–2004   Tartu Ülikool, Botaanika ja Ökoloogia Instituut, tehnik
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Peamised uurimisvaldkonnad:
Valguskohanemine taimedel, primaarproduktsiooni hindamine kaugseire meetodeil, kliimamuutuste mõju taimedele

Publikatsioonide loetelu:
Mänd P, Hallik L, Peñuelas J, Kull O. 2013. Electron transport efficiency at opposite leaf sides: effect of vertical distribution of leaf angle, structure, chlorophyll content and species in a forest canopy. *Tree Physiology* 33: 202–210.

Mänd P, Hallik L, Peñuelas J, Nilson T, Duce P, Emmett BA, Beier C, Estiarte M, Garadnai J, Kalapos T, Schmidt IK, Kovács-Láng E, Prieto P, Tietema A, Westerveld JW, Kull O. 2010. Responses of the reflectance indices PRI and NDVI to experimental warming and drought in European shrublands along a north–south climatic gradient. *Remote Sensing of Environment* 114: 626–636.

Beier C, Emmett BA, Tietema A, Schmidt IK, Peñuelas J, Kovács Láng E, Duce P, DeAngelis P, Gorissen A, Estiarte M, de Dato GD, Sowerby A, Kröel-Dulay G, Lellei-Kovács E, Kull O, **Mänd P**, Petersen H, Gjelstrup P, Spano D. 2009. Carbon and nitrogen balances for 6 shrublands across Europe. *Global Biogeochemical Cycles* 23: 1–13.

Riikonen J, Syrjälä L, Tulva I, **Mänd P**, Oksanen E, Poteri M, Vapaavuori E. 2008. Stomatal characteristics and infection biology of *Pyrenopeziza betulicola* in *Betula pendula* trees grown under elevated CO_2 and O_3. *Environmental Pollution* 156: 536–543.

Eichelmann H, Oja V, Rasulov B, Padu E, Bichele I, Pettai H, **Mänd P**, Kull O, Laisk A. 2005. Adjustment of leaf photosynthesis to shade in a natural canopy: reallocation of nitrogen. *Plant, Cell and Environment* 28: 389–401

Muud teaduslikud publikatsioonid ja osalemine toimetustöös:
Tulva I, Öpik M, **Mänd P** (toim.). 2006. Pärandumise teooria. *Schola Biotheoretica XXXII*. Eesti Loodusuurijate Selts, OÜ Sulemees, Tartu
Mänd P, Tulva I. 2004. Globaalset süsinikuringet rihti ajamas. *Schola Biotheoretica XXX*. Tasakaalu Teooria, toim. Tulva I, Öpik M, Puura I. Tartu, OÜ Sulemees, pp. 126–128
Kupper P, **Mänd P**, Tulva I. 2003. Ehast koiduni: kas taim magab sügavalt? *Schola Biotheoretica XXIX*. Puhkuse teooria, toim.Tammaru T, Puura I. Tartu, OÜ Sulemees, pp. 21–25

Preemiad ja stipendiumid:
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- Stipendium osalemaks konverentsil Tšehhis, Olomouc 2006
- Reisistipendiumid osalemaks NordForsk doktorikoolis Soomes, Joensuu 2004 ja Rootsis, Umea 2005
- Stipendium osalemaks ESP kongressil Norras, Lillehammer 2001
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- Eesti üliõpilaste teadustööde riikliku konkursi III preemia, 2000

Muu teaduslik organisatsiooniline ja erialane tegevus:

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- Botaanika osakonna uurimisteemasid populaarsel viisil tutvustava veebilehe tegemise kordineerimine ja ökofüsioloogia õppetooli uurimissuundi tutvustava veebilehe tegemine ning Botaanika osakonda tutvustava seminari korraldamine bakalaureuse tudengitele, 2007
- Iganädalase bioloogia kraadiõppurite seminari "Journal club" korraldamine 2006/2007
- Põhjamaade võrgustiku Carbon Dynamics in Managed Terrestrial Ecosystems (NordForsk) ja Maateaduste ja ökoloogia doktorikooli PhD kursuse korraldusmeeskonnas. Tree canopy – structure and functioning – from below and above. 3.–14. september 2006, Järvselja ja Vihula, Eesti
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