DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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LEA HALLIK

Generality and specificity in light harvesting, carbon gain capacity and shade tolerance among plant functional groups

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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. Hallik L, Niinemets Ü, Wright I. 2009. Are species shade and drought tolerance reflected in leaf-level structural and functional differentiation in Northern Hemisphere temperate woody flora? *New Phytologist* doi: 10.1111/j.1469- 8137.2009.02918.x (in press)

II. Hallik L, Kull O, Niinemets Ü, Aan A. 2009. Contrasting correlation networks between leaf structure, nitrogen and chlorophyll in herbaceous and woody canopies. *Basic and Applied Ecology* **10**: 309–318.

III. Aan A, Hallik L, Kull O. 2006. Photon flux partitioning among species along a productivity gradient of an herbaceous plant community. *Journal of Ecology* **94**: 1143–1155.

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The participation of the author in preparing the listed publications is as follows:

Paper I – performed statistical analysis and was lead author in writing the paper.
Paper II – gathered the data, performed statistical analysis and was lead author in writing the paper.
Paper III – gathered the data and participated in writing.

LIST OF ABBREVIATION

A_a	light-saturated photosynthetic capacity per unit leaf area (μmol m^{-2} s^{-1})
A_m	light-saturated photosynthetic capacity per unit leaf dry mass (nmol g^{-1} s^{-1})
aNUE	above-ground nitrogen use efficiency, defined as above-ground dry mass per unit of total leaf nitrogen (g $g(N)^{-1}$)
Chl_a	chlorophyll content per unit leaf area (g m^{-2})
Chl/N	ratio of chlorophyll to nitrogen contents
DB	deciduous broad-leaved woody species of temperate Northern Hemisphere
EB	evergreen broad-leaved woody species of temperate Northern Hemisphere
EC	evergreen conifers of temperate Northern Hemisphere
I_D	relative penetration of diffuse irradiance on the horizontal plane
LAR	leaf area ratio, defined as leaf area per unit of above-ground biomass (m^2 g^{-1})
LL	mean leaf life-span (mo)
LMA	leaf dry mass per unit area (g m^{-2})
LUE	light use efficiency, defined as productivity per unit of absorbed light (g mol^{-1})
N_a	nitrogen content per unit leaf area (g m^{-2})
N_m	leaf nitrogen content per unit dry mass (%)
NUE	nitrogen use efficiency, defined as productivity per unit of nitrogen taken up from soil (g $g(N)^{-1}$)
PNUE	photosynthetic nitrogen-use efficiency, defined as an instantaneous rate of carbon fixation per unit of plant nitrogen (μmol $g(N)^{-1}$ s^{-1})
PCA	principal components analysis
Rubisco	ribulose-1,5-bisphosphate carboxylase/oxygenase
Φ_M	light absorption per unit of above-ground biomass (mol g^{-1} day^{-1})
Φ_N	light absorption per unit of leaf nitrogen (mol $g(N)^{-1}$ day^{-1})

INTRODUCTION

Various environmental constraints – shortage and excess of light or water, low or high temperature, mineral deficiency, salinity – limit photosynthetic production in natural plant communities. Ecologists traditionally define any suboptimal conditions which limit the rate of plant growth as a stress situation (Grime, 1977). The term 'stress' is also widely used among plant physiologists referring mainly to the unstable physiological state of an organism (Larcher, 1987; Gaspar *et al.*, 2002). When interpreting the shortage of light as a resource limitation, it is important to consider that shade conditions are generally created by the vegetation itself. Therefore low light availability can coincide both with plenty of available soil resources, but also with the lack of mineral nutrients, if soil becomes depleted as nutrients are accumulated into biomass.

Plant species vary widely in their tolerance to different environmental stress conditions (Grime, 1977; Tilman, 1988; Bigelow & Canham, 2002). Enhanced stress tolerance is generally associated with species-specific leaf traits, which improve persistence and longevity – for instance longer leaf life-span (LL), higher leaf dry mass per unit area (LMA), lower leaf nitrogen content and lower photosynthetic capacity (Westoby *et al.*, 2002). Higher species-specific LMA is usually accompanied by prolonged average leaf longevity (Reich *et al.*, 1997; Reich *et al.*, 1999). This strong association is commonly explained by greater structural toughness of high LMA leaves, which allow them to cope with biological and physical hazards like herbivory and wind damage (Reich *et al.*, 1991; Wright & Cannon, 2001). LMA can be viewed as a product of two components – leaf density and thickness. Larger fraction of relatively nitrogen-poor mechanical tissues in leaves, such as collenchyma and sclerenchyma increases tissue density (Garnier *et al.*, 1997). Hence the high LMA due to increased tissue density is associated with reduced leaf nitrogen concentration and photosynthetic capacity (Niinemets, 1999), particularly if expressed per unit of leaf dry mass. The fraction of mechanical tissues in leaf tends to decrease with increasing leaf thickness (Garnier *et al.*, 1999). High LMA due to increased leaf thickness, therefore, is associated with increased leaf nitrogen content and photosynthetic capacity (Niinemets, 1999), particularly if expressed per unit of leaf area.

Within a given species, leaves developed at high light are thicker and exhibit higher LMA than those grown in shaded conditions. Whether species-specific LMA of shade-tolerant species is lower than that of shade-intolerant species under common irradiance, is less clear and contrasting reports can be found in the literature. Shade tolerance has been traditionally thought to depend on traits, which improve light harvesting efficiency (Valladares & Niinemets, 2008). As low LMA allows to construct larger foliar area per unit biomass, it has been hypothesized that more shade tolerant species have lower LMA than intolerants (Givnish, 1988). Some reports are consistent with this hypothesis, showing that at least among deciduous species, shade tolerators do have lower LMA at common irradiance (Beaudet & Messier, 1998; Kull & Niinemets, 1998;

Niinemets, 2006), but not among evergreens (Lusk *et al.*, 2008). Based on the work in seedlings, Reich *et al.* (2003) strongly suggests opposite to the common expectation, that shade tolerant species grown under the same light conditions have higher LMA than intolerants, and conclude that species shade tolerance is associated with general resource-conservation syndrome traits, which include long leaf life-span, high LMA, low mass-based leaf nitrogen content, low photosynthetic capacity and low respiration rate. This discrepancy between studies has been associated with ontogenetic modifications in biomass allocation and LMA (Niinemets, 2006). Shade intolerant species commonly have smaller seeds and therefore, at common age, seedlings of shade intolerant species have lower mass and smaller LMA and greater fraction of biomass in leaves (Niinemets, 2006).

Aside water, which is the key environmental factor most often constraining terrestrial productivity, nutrients are the second key limitation. Among soil nutrients, nitrogen has usually the strongest effect on both plant productivity and biomass allocation (Vitousek & Howarth, 1991). Optimality models show that for a given amount of nitrogen in foliage, the carbon gain of the entire canopy is maximized when foliar nitrogen is distributed proportionally to light availability along the vertical canopy profile (Field, 1983; Sands, 1995). This is because leaf nitrogen content is strongly related to the leaf photosynthetic capacity (Evans, 1989) and leaves with higher carbon assimilation capacity can use stronger light more efficiently for carbon assimilation. The common explanation for the strong relationship between total leaf nitrogen content and photosynthetic capacity is the fact that a large fraction of leaf nitrogen is allocated into photosynthetic apparatus, particularly into ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the primary enzyme of photosynthetic carbon assimilation cycle (Evans, 1993a; Hikosaka & Terashima, 1996). However, proteins in leaf are continuously turned over by simultaneous synthesis and degradation. The permanent turnover of proteins consumes energy, and as the mature leaves cannot import carbohydrates due to the physiological and anatomical restrictions (Turgeon, 1989), the strong relationship between foliar nitrogen and photosynthetic performance can mean that certain amount of energy must be captured through photosynthesis to maintain the nitrogen within the leaf (Kull, 2002).

The utilization of nitrogen and light are often also viewed in terms of their use efficiency either at a single leaf, whole plant or ecosystem level. The efficiency of using nitrogen (NUE), taken up from soil, for dry biomass production by plants combines two distinct components: (i) photosynthetic nitrogen-use efficiency (PNUE) defined as the instantaneous rate of carbon fixation per unit of plant nitrogen, and (ii) the mean residence time (MRT), which determines the duration of return from a unit of nitrogen invested (Berendse & Aerts, 1987). In practice, the inverse of the nitrogen concentration in the biomass is commonly used as a rough estimate of plant NUE (Chapin, 1980; Shaver & Melillo, 1984). Light absorption per unit of leaf nitrogen (Φ_N) was originally also used as an indicator of NUE (Hirose & Werger, 1994), but this approach is valid only if the light-use efficiency (LUE, productivity per unit of absorbed light) remains constant, as Φ_N equals the ratio of instantaneous NUE to LUE. Based on model calculations (Kull & Jarvis, 1995; Kull & Kruijt, 1999) Φ_N can be interpreted as the energetic cost of maintaining nitrogen within the foliage. Light capture per unit of above-ground biomass (Φ_M) can be used as an estimation of plant efficiency to acquire the light resource with the above-ground biomass regarded as an investment to capture light (Hirose & Werger, 1995). However, if biomass is viewed as a productivity over a certain time period, low Φ_M should be interpreted as an evidence of increased LUE. If light energy is efficiently converted into biomass, light absorption per unit of biomass should decline even if available light resources do not change; and increased amount of the photosynthesising tissue per unit of intercepted light leads to an increase in LUE as with the increasing amount of photosynthetic apparatus, a relatively smaller proportion is light saturated (Kull, 2002).

Photosynthetic apparatus consists of two major fractions: (i) light-reactions of photosynthesis are responsible for the capture of light energy and using it to make energetic (ATP) and reductive equivalents (NADPH), and (ii) dark reactions utilize high-energy molecules for carbon fixation. As chlorophyll-binding protein complexes can be found only in light-harvesting part, while the largest fraction of leaf nitrogen is in Rubisco, i.e. in the biochemical part of the photosynthetic machinery, chlorophyll to nitrogen content ratio (Chl/N) reflects the relative share of light-harvesting part of the photosynthetic apparatus. At very low light photosynthesis increases linearly with increasing light intensity, but starts to deviate from the linear relationship as soon as photosynthesis in the uppermost chloroplasts reaches light saturation. This earlier saturation of photosynthetic apparatus near upper leaf surface is an universal phenomenon. Both at single leaf level (Nishio *et al.*, 1993; Han *et al.*, 1999) and within the canopy (Sinclair & Shiraiwa, 1993), the increasing thickness of photosynthetic tissue (i.e. greater LMA) enchances LUE as relatively smaller fraction of it becomes light saturated (Kull, 2002). In low-light environments, the leaves invest relatively more into the light harvesting part of the photosynthetic machinery, reflected in increased Chl/N ratio. Despite of rapid increases at very low light availability, the Chl/N ratio remains still lower, than the predicted optimum for maximising the photosynthesis in the lowest canopy layers (Evans, 1993b; Kull & Kruijt, 1998). The ability of photosynthetic apparatus to acclimate, is also limited in the case of very high irradiance, as Chl/N ratio tends to achieve a plateau (Kull & Niinemets, 1998). Apparently there are certain construction limits which do not allow the amount of light harvesting antenna to be reduced or increased sufficiently for full acclimation to extreme shade or very high irradiance (Evans, 1993b; Kull, 2002).

The remote sensing methods detect primarily the chlorophyll content of the upper canopy layers, which dominate in the reflectance signal above the vegetation, and with some assumptions also the total canopy chlorophyll content can be estimated from the vegetation reflectance data relatively well (Filella & Peñuelas, 1994; Sims & Gamon, 2002; Coops *et al.*, 2003; le Maire *et* *al.*, 2004). However, for using remote sensing information to parameterize large-scale carbon gain models (Sellers *et al.*, 1992; Dai *et al.*, 2004) whole canopy photosynthetic capacity has to be estimated from reflectance data, and the foliage photosynthetic potential is usually related more strongly to canopy nitrogen than to chlorophyll content (Evans, 1989). Therefore further assumptions about the correlation between N_a and Chl_a are needed to predict N_a and foliage photosynthetic capacities from remotely-assessed chlorophyll content (Schepers *et al.*, 1998; Weih & Rönnberg-Wästjung, 2007). Positive scaling of N_a with light availability has been postulated to reflect optimal distribution of limiting nutrients in the canopy, as it maximises canopy photosynthesis for a given total canopy nitrogen (Anten, 2005). To predict the nitrogen profiles from remote sensing data, the assumption of an "optimal" distribution of nitrogen or arbitrary correlations between nitrogen and current leaf light environment would be the most feasible approach (Friend, 2001; Dai *et al.*, 2004).

To improve the accuracy of large-scale carbon gain model estimations based on remotely-assessed chlorophyll content, more data about the vertical distribution profiles of chlorophyll and nitrogen within canopy is currently needed. For large-scale conclusions it is also important to gain more advanced insight into generality and specifity of plant responses among life-forms, functional groups and species. Responses observed at community level consist of both physiological plasticity within species and species-specific differences. Heterogeneous distributions of resources and competitors have lead to diversity of plant species and traits to cope with different habitats. Among functional groups of woody species with different leaf longevity deciduous broad-leaved species and evergreen conifers co-exist in cooler habitats while evergreen broad-leaved angiosperms are more common in warm temperate climate.

Aims

The general aim of this study was to identify the suites of traits responsible for species shade tolerance and light harvesting in different plant functional groups. In particular, to understand how plant responses to light availability depend on species-specific functional traits in different plant functional groups at common light availability (genotypic plasticity) and within light gradients (phenotypic patterns). First we hypothesize that among woody species, higher shade tolerance is associated with species-specific leaf traits, which promote foliar area accumulation and/or reduce the 'cost' of leaf production (longer leaf life-span, smaller dry mass per area, lower nitrogen content and lower photosynthetic capacity). We also expect that in the herbaceous canopy community-level light capture efficiency per unit biomass and leaf nitrogen, is modified by changes in species composition, and that species dominating at different soil fertility have different strategies for biomass and nitrogen partitioning.

The specific aims of this thesis were:

(1) to examine how leaf life-span, leaf dry mass per area, leaf nitrogen content and photosynthetic capacity are related to species shade tolerance in temperate woody species of the Northern Hemisphere and how these patterns vary among plant functional groups;

(2) to compare the responses of deciduous tree species and herbaceous species regarding the distribution patterns of leaf chlorophyll and nitrogen contents and leaf dry mass per area with the light availability gradient within the canopy;

(3) to examine how light capture ability varies in the herbaceous canopy with respect to biomass and nitrogen partitioning patterns along a productivity gradient; to which extent the community-level variation of light absorption per unit of above-ground biomass and per unit of leaf nitrogen can be contributed to changes in species composition; and which species-specific characteristics of biomass and nitrogen partitioning lead to dominance of a species in different soil conditions.

MATERIALS AND METHODS

The first paper is based on the literature data published for a number of temperate woody species in the Northern Hemisphere. The other two papers are based on original field measurements in south-eastern Estonia, conducted in a grassland (Aru, near town of Elva: 58°16'N, 26°18'E) and a mixed deciduous forest (Järvselja: 58°22'N, 27°20'E).

Literature-based data

Information from three main databases (Niinemets, 1999; Wright *et al.*, 2004; Niinemets & Valladares, 2006) were combined to generate the database of species shade tolerances and leaf traits on 339 woody species from entire temperate zone of the Northern Hemisphere. The information on the species' shade tolerance scores was provided by the database of Niinemets and Valladares (2006), which contains cross-calibrated tolerance rankings for 806 temperate woody species from Europe, East-Asia and North-America. Shade tolerance, in this database is defined as the approximate minimum light intensity at which a given species is able to grow. Shade tolerance rank 1 corresponds to very intolerant (minimum light availability at least 50% of full sunlight) and 5 to very tolerant (minimum light requirement 2–5%).

The information on species-specific values of leaf structural and physiological traits – leaf dry mass per area (LMA), nitrogen content and photosynthetic capacity – were obtained from the databases of Wright *et al.* (2004) and Niinemets (1999). Only the data of upper-canopy leaves, developed under high-light conditions were used in these databases for calculating the average species-specific leaf characteristics. Glopnet database (Wright *et al.*, 2004) provided information for 1978 species from 175 sites and the database of Niinemets (1999) for 597 woody species from 182 sites. Out of these species, 339 were present in the database of shade tolerance rankings (Niinemets & Valladares, 2006), which set the limit to the number of species in combined dataset of species shade tolerances and leaf traits.

Leaf life-span (LL) used here, is an average leaf life-span, but not the maximum possible leaf longevity. As the two main databases used (Niinemets, 1999; Wright *et al.*, 2004), provided the data for mean leaf life-span only for 148 species, missing values of LL were obtained from 42 additional literature sources, by counting the average number of leaf cohorts with at least 50% foliage remaining for evergreens, and on the basis of growing season length and the number of leaf flushes for deciduous species (see paper I, Appendix A1 for detailed description of collection of leaf life-span data).

Measurements in the forest site

The measurements in the mixed deciduous forest located in south-eastern Estonia at Järvselja. The site was dominated by two shade intolerant early-successional species, *Betula pendula* Roth. (shade tolerance score = 2.03 according to Niinemets & Valladares, 2006) and *Populus tremula* L. (shade tolerance = 2.22) in the upper canopy layer (20–27 m) and by a shade tolerant species *Tilia cordata* Mill. (shade tolerance = 4.18) in the lower layer (15–20 m). Permanent scaffolding towers were used to access the foliage. Four to five sample points were chosen along the vertical light gradient at different heights in the canopy of each studied species. To estimate the light availability, relative diffuse irradiance (I_D) was calculated from hemispherical photographs taken above each sample point (Nikon CoolPix 950 digital camera equipped with an FC-E8 “fish-eye” conversion lens, Nikon Corporation, Tokyo, Japan; images were analysed with Winscanopy 2001a Pro, Regent Instruments Inc., Quebec, Canada). Area of leaf lamina, dry mass, nitrogen and chlorophyll contents were assessed for each species from all sample points.

The site description and measurements in the grassland

The herbaceous community located in south-eastern Estonia near Elva was a former agricultural field abandoned five years earlier. Ten 1×1 m plots were established along the slope (inclination angle ca. 5°) of a small hillock that produced a gradient in soil conditions, the most apparent in the thickness of the humus horizon (see detailed description in Paper III). The species growing in sample plots were *Achillea millefolium* L., *Agrostis gigantea* Roth, *Agrostis stolonifera* L., *Anthriscus sylvestris* (L.) Hoffm., *Cerastium vulgare* Hartm., *Cirsium arvense* (L.) Scop., *Dactylis glomerata* L., *Elymus repens* (L.) Gould, *Festuca pratensis* Huds., *Festuca rubra* L., *Helictotrichon pubescens* (Huds.) Pilger, *Phleum pratense* L., *Pilosella officinarum* F.W. Schultz et Sch. Bip., *Polygala vulgaris* L., *Potentilla anserina* L., *Ranunculus acris* L., *Taraxacum officinale* Weber ex Wigg, *Trifolium pratense* L. and *Vicia cracca* L. Depending on the height of the vegetation, the canopy was divided into three to five layers, each 15–25 cm thick. To characterize the vertical gradient in light conditions, a series of measurements were made above and below each canopy layer with a LI-191 line quantum sensor (Li-Cor Biosciences, Lincoln, NE, USA). To characterize the variation in the diffuse component of solar radiation, one set of measurements were made before sunrise. Leaf angles were measured (using a protractor) for major species in all plots and layers. Then the biomass in each canopy layer was harvested within a 0.5×0.5 m area in the centre of the sample plot and sorted by species. Leaf and stem dry mass, leaf area, chlorophyll and nitrogen contents were assessed separately for each species and canopy layer. Light absorption partitioning between species was calculated using modified approach of Anten and Hirose(1999), separately for each canopy layer based on the measurements of direct and diffuse irradiance, leaf area, leaf angle distribution and chlorophyll content, accounting for light absorption by stems and foliage clumping. The exact formulae are shown in Paper III.

Chlorophyll and nitrogen determination

Chlorophyll concentration of a sample was measured optically in 80% aqueous acetone with a S2000-FL spectrometer (Ocean Optics, Dunedin, FL, USA) following the equations of Porra *et al.* (1989). Nitrogen concentration was determined using a standard Kjeldahl method by Kjeltec Auto 1030 analyser (Foss Tecator AB, Höganäs, Sweden).

RESULTS AND DISCUSSION

‘Leaf economics spectrum’ and shade tolerance in temperate woody species of the Northern Hemisphere

To explore how mean leaf life-span (LL), leaf dry mass per area (LMA), leaf nitrogen content (N) and photosynthetic capacity (A) were related to the species tolerance to low light availability an extensive database consisting of 339 woody species from temperate Northern Hemisphere was constructed. This database contained data on 244 deciduous broad-leaved angiosperm species (denoted as DB functional group), 50 evergreen broadleaved angiosperms (EB), 35 evergreen conifers (EC), 7 evergreen needle-leaved angiosperm species and 3 deciduous conifers. The two smallest groups (evergreen needle-leaved angiosperm species and deciduous conifers) were included in the analyses of the pooled data and these two minor groups were not outliers in any of the broad relationships (data not shown), but separate analyses within the functional groups were conducted only for the three major groups (DB, EB and EC).

Across the whole dataset, LL was positively associated with LMA (Pearson's correlation coefficient $r =$ 0.81, $p < 0.0001$) and negatively with leaf nitrogen per dry mass, N_m ($r = –0.71$, $p < 0.0001$) and photosynthetic capacity per leaf dry mass, A_m ($r = –0.83$, $p < 0.0001$). This strong coordination of leaf functional traits – LL, LMA, N_m and A_m – at a global scale, is called 'leaf economics spectrum'. This spectrum spans from 'quick-return' strategy characterised by short-living leaves with low dry mass investments per leaf area and high photosynthetic capacities to 'slow-return' strategy characterised by long leaf life-span and greater structural toughness of leaves, which results in high LMA, low N_m and low A_m (Wright *et al.*, 2004). The intriguing question would be whether the variation in shade tolerance is compatible with the general strategies of stress-tolerant and intolerant species, as it has been earlier suggested by Reich *et al.* (2003). To reduce the four-dimensional set of leaf traits forming ‘leaf economics spectrum’ to one-dimensional trait characterising species strategy along the continuum of ‘quick-return’ to ‘slow-return’ spectrum, principal components analysis (PCA) was conducted for LL, LMA, N_m and A_m on pooled data of 339 species. The results of PCA (Table 4 in I) showed that 83% of the total variation in LL, LMA, N_m and A_m was described by the first axis. Factor scores from this first PCA axis were used in subsequent correlation analysis as a variable characterising the species strategy for resource availability in general (the slow-return species at one end of the ‘leaf economics spectrum’ representing the general strategy for coping with limited resources and the fast-return species at the other end of the spectrum representing the strategy for high resource availability). However, the lack of correlation between the factor scores from the first PCA axis and species shade tolerance rankings (Table 5 in I) showed that contrary to the expectations in literature, the species ability to tolerate limited light availability is not related to the global-scale gradient of 'leaf economics'.

Mean species-specific leaf traits and shade tolerance within functional groups (DB, EB and EC)

In order to understand, why species shade tolerance was not related to the general ‘leaf economics spectrum’, the bivariate relationships between the shade tolerance ranking and individual leaf traits were further investigated. Contrary to the global pattern of 'leaf economics' where LL and LMA are expected to scale positively with each other, species shade tolerance increased with LL (pooled data: $r = 0.21$, $p < 0.001$; within DB group: $r = 0.30$, $p < 0.001$; EB group: $r = 0.33$, $p < 0.05$; EC group: $r = 0.68$, $p < 0.001$) and decreased with LMA (pooled: $r = –0.12$, $p < 0.05$; DB: $r = –0.39$, $p < 0.001$; EB: $r = –0.36$, $p < 0.05$; EC: $r = –0.49$, $p < 0.001$). In pooled data, shade tolerance also decreased with nitrogen content per leaf area (N_a: $r = –0.26$, $p < 0.001$) and photosynthetic capacity per leaf area (A_a: $r = –0.42$, $p < 0.001$).

Phenotypic plasticity enables the leaves developed in shaded conditions to have lower LMA than ‘sun-leaves’ within the same tree crown (Fig. 1A in II). If the selection pressure along light availability gradient favours low LMA in shaded conditions, it should lead to inherently lower LMA of shade-tolerant species compared to intolerants. It has been hypothesized that lower LMA in shade-tolerant species is an important adaptive trait, which reduces the biomass requirement for the construction of unit foliar area (Givnish, 1988). Among winter-deciduous temperate trees a negative relationship between species-specific LMA and shade tolerance has been often observed, in particular if ontogenetic variations are considered (Niinemets, 2006; Lusk & Warton, 2007), while the scaling between LMA and shade tolerance has been suggested to be positive among evergreen species due to the effect of leaf longevity (Lusk *et al.*, 2008). Longer leaf life-span has been postulated to be adaptive under shade conditions due to the increased foliar area by the accumulation of leaf cohorts produced over several years in evergreens, and because of leaf longevity also determines the duration of return from unit of investment into photosynthetic tissues (Lusk, 2002; Westoby *et al.*, 2002). As LL and LMA scale positively with each other at global scale, it is expected that among the evergreens the shade-tolerant species should have higher LMA due to the positive association between LL and shade tolerance (Lusk & Warton, 2007; Lusk *et al.*, 2008). Among the temperate woody species studied here (Table 2 in I), shade tolerance was inversely related to LMA also within the evergreen groups, however, contrary to the global pattern, within evergreen groups LL and LMA were not significantly related (Fig. 1A; EB: $r = 0.17$, $p > 0.05$; EC: $r = –0.02$, $p > 0.05$).

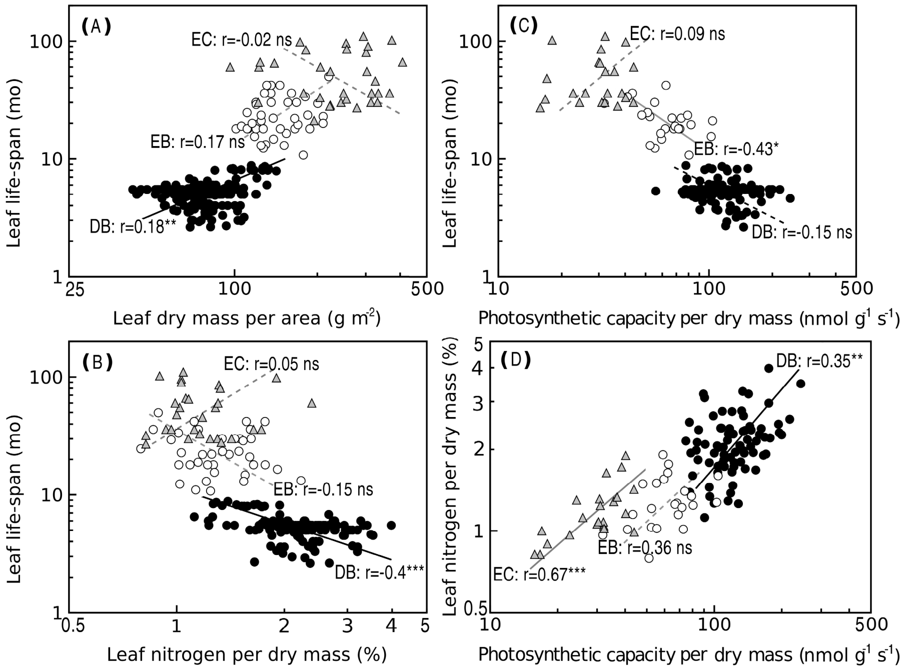

Figure 1. Bivariate relationships between the four leaf traits forming 'leaf economics spectrum'. Data were separately fitted by standardised major axis regressions within major functional groups in temperate Northern Hemisphere woody flora (deciduous broadleaved angiosperms – DB; evergreen broadleaved angiosperms – EB and evergreen conifers – EC) and Pearson's correlation coefficients (*r*) within each group are shown with significance coded as *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns $p > 0.05$.

The species shade tolerance was clearly related to LL and LMA within each functional group (Table 2 in I) and all three major functional groups differed significantly by mean values of LL, LMA and A_m (Fig. 2). DB group was characterised by the lowest LL and LMA, and the highest A_m, EB group exhibited intermediate values and EC functional group had the highest LL and LMA accompanied by the lowest A_m. The differences between DB and EC group were so pronounced that even the ranges of LL and A_m values did not overlap (Fig. 2, the whiskers denote minimum and maximum values). However, at the same time, the mean shade tolerance did not differ significantly between the three major functional groups and nearly whole range of shade tolerance scores (from 1 corresponding to very intolerant to 5 corresponding to very tolerant species) were present within each group (Fig. 2 inset). Therefore it seems that despite the strong global-scale coordination among plant functional traits forming the 'leaf economics spectrum', there is still enough room for ecological differentiation, as various alternative combinations of different values of the same traits can result in similar tolerance.

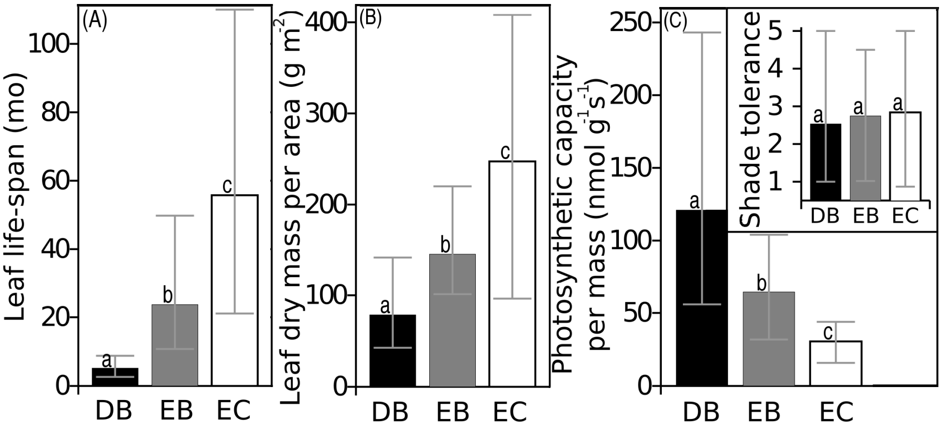

Figure 2. The comparison of three main functional groups (deciduous broadleaved angiosperms – DB; evergreen broadleaved angiosperms – EB and evergreen conifers – EC) in the database of temperate Northern Hemisphere woody species. The bar heights show the mean trait values within the groups and the whiskers illustrate the whole span of variation, corresponding to the maximum and minimum value within the given functional group. Means with the same letter are not significantly ($p > 0.05$) different between the functional groups (Games-Howell test).

There were remarkable differences between the strategies exploited within functional groups to achieve the plant tolerance to shade. As winter-deciduous species cannot prolong the leaf longevity to a great extent due to the limitation by the length of the growing season, but this group is generally characterised by high photosynthetic capacities (Fig. 2C); the strategy of deciduous broad-leaved group appeared to be reducing the construction cost of the unit of leaf area to increase the shade tolerance. Within the deciduous broad-leaved group shade tolerance was negatively related to nitrogen content per leaf area (N_a: $r = –0.47$, $p < 0.001$) and photosynthetic capacity (both mass based A_m: $r = –0.47$, $p < 0.001$ and area based A_a: $r = –0.61$, $p < 0.001$). Hence it appears that besides the controversial trends in LL and LMA, which were present in all groups, the combination of the leaf traits enhancing shade tolerance in deciduous broad-leaved group, contradicts the general pattern of 'leaf economics spectrum' (Table 4 in I, Fig. 1) also concerning the simultaneous reduction of LMA and A_m with increasing shade tolerance of the species (Table 2 in I).

Contrary to deciduous species, in evergreen conifers group, which was characterised by the longest leaf life-span (Fig. 2A), species shade tolerance was increasing with A_m ($r = 0.56$, $p < 0.001$) and photosynthetic nitrogen use efficiency (PNUE, $r = 0.50$, $p < 0.001$). It has been suggested that worldwide conifers are mainly constrained to less productive sites due to their lower photosynthetic capacities compared to angiosperm trees and lower fractions of foliar nitrogen in photosynthetic machinery (Lusk *et al.*, 2003). However, as photosynthetic capacity of shade-tolerant deciduous angiosperms is expected to be lower than average for deciduous angiosperms, it may offer some explanation to how several shade tolerant conifers (members of genera *Abies*, *Taxus* and *Tsuga*) can still successfully compete with angiosperms in dense forests on fertile sites.

Evergreen broad-leaved group with intermediate leaf longevity (Fig. 2A), also exhibited intermediate strategy in respect of shade tolerance compared to deciduous broad-leaved species and evergreen conifers (Table 2 in I). Although there exists a global-scale coordination of leaf traits, which are individually also related to species shade tolerance, it appears that primarily the strategy, how to achieve shade tolerance, not the tolerance itself changes along the 'leaf economics spectrum'. Alternative strategies can also offer some insight into the geographical distribution of the species, as mixed forests of winter-deciduous broad-leaved and evergreen coniferous species are common in cool temperate climates, while evergreen broad-leaved trees become gradually dominating in warmer temperate forests.

Acclimation to a vertical gradient of light availability in herbaceous and deciduous woody canopies

Besides the differences in species-specific leaf traits discussed in the previous chapter assessed at high light availability (genotypic plasticity), the species and functional groups may also significantly vary in the capacity for foliage acclimation to light gradients. Such responses to changes in the environment are called phenotypic plasticity.

To understand the mechanisms and possible limitations of light acclimation within herbaceous and woody canopies the distribution of LMA, leaf chlorophyll and nitrogen contents along vertical gradient of light availability were investigated in herbaceous species from an old-field and in three deciduous tree species with different shade tolerance (*P. tremula, B. betula* and *T. cordata*). The range of light conditions measured in July was similar in the studied tree and herbaceous canopies varying from 1 above the canopy to 0.1–0.2 measured above the lowest layer.

The results of paper I showed that shade-tolerant deciduous trees had lower species specific LMA and N_a compared to intolerants. Among deciduous woody species appears to be strong similarity between plastic and evolutionary responses of these leaf traits to light gradients when to compare the species specific results of paper I with the phenotypic plasticity along the vertical gradient of light availability within the canopy studied in paper II (Fig. 1 in II). Both LMA and N_a were positively related to light availability within the canopy in studied tree species (r ranging from 0.83 to 0.93, $p < 0.001$), but for grassland species these correlations were generally insignificant with only few exceptions (Table 1 in II). However, despite the weak relationship with light availability in herbaceous species, the positive scaling of N_a with LMA was common for all data in paper II (Fig. 2A in II), and the correlation between LMA and N_a was strong both for all three tree species pooled ($r = 0.94$, $p < 0.001$) and for all herbaceous species pooled ($r = 0.84$, $p < 0.001$). The results of path analysis in paper II showed that the light-dependent modifications in N_a were predominantly controlled by the variation of LMA (Fig. 3 in II).

LMA is one of the most extensively studied foliar trait as it measures the biomass investment per unit of leaf area, and it is known to be determined first of all by light conditions during leaf development (Niinemets, 2007). In deciduous tree canopies perennial branching framework remains for many years and majority of leaves are formed at approximately the same time period in the beginning of the growing season. As the leaf production is negligible during the rest of the growing season in these deciduous tree species, which we investigated, the main changes in light availability occur before the leaf reaches to full maturity. Although the light gradient becomes notably steeper during leaf expansion growth, lower canopy leaves experience somewhat lower light availability than upper canopy leaves already since the formation and hence the light gradient throughout the rest of the leaf life-span can reflect the light availability patterns during leaf development. Leaves of *P. tremula* and *T.cordata* achieve their final LMA ca. 40–50 days after bud-burst (Niinemets *et al.*, 2004). In contrast, the foliage in herbaceous canopy undergoes much more dramatic changes during its life-span, as plants grow taller forming constantly new leaves and stems, while lower leaves and smaller (subordinate) individuals become gradually shaded (Anten *et al.*, 1998).

The within-canopy pattern in N_a can result either from light-dependent modifications in LMA, or from changes in nitrogen content per unit of leaf dry mass (N_m), but the modifications in N_m have been shown to reflect leaf senescence (Field, 1983; Hirose & Werger, 1987; Anten *et al.*, 1998). The rapid decline in N_m of the leaves in deciduous tree-canopy due to senescence occurs in autumn at the end of the growing season (Niinemets *et al.*, 2004) but our measurements were made in July and hence no effect of senescence can be expected in tree canopy. However, in herbaceous species, the content of Rubisco starts to decline already a few days after full foliage expansion (Hidema *et al.*, 1991; Hikosaka *et al.*, 1993; Ono *et al.*, 2001; Murchie *et al.*, 2005), reflecting the onset of leaf nitrogen reallocation from senescing foliage. Furthermore, light environment can substantially influence leaf aging process. Shading the whole plant delays leaf senescence, as demonstrated by experiments, while shading individual leaves or branches accelerates senescence via re-translocation of foliar nitrogen (Hikosaka, 2005; Niinemets, 2007). However, the re-allocation of nitrogen from older shaded foliage to new leaves in upper canopy was not sufficient to produce the detectable vertical gradient of leaf nitrogen with increasing light availability in herbaceous species in our study (Table 1 in II). But the variability of N_m within a given species was remarkably lower among the tree species compared to the herbaceous plants (Table 2 in II), suggesting that at some limited rate the nitrogen re-translocation from older leaves was occurring in herbaceous canopy.

Average values of LMA and N_a were larger in trees than in herbaceous plants at the same light availability, and these differences became more pronounced at high irradiance (Fig. 3). As in herbaceous canopy new leaves, formed in upper layers, are likely to become shaded later, it may be not beneficial to produce the leaves with fully high light-acclimated traits (including high LMA and N_a) even under conditions of high irradiance.

Mature leaves have only a limited ability to modify leaf anatomy, however, these leaves have a significant capacity to adjust leaf chlorophyll content and the fraction of leaf nitrogen involved in light harvesting (Chl/N ratio) in response to changed light conditions (Brooks *et al.*, 1996; Oguchi *et al.*, 2003). Acclimation of leaf chlorophyll content to high irradiance consists of two opposite responses as confirmed by the results of path analysis (Fig. 3 in II). Increased irradiance can lead to enhanced leaf chlorophyll content via changes in leaf anatomy, like increased number of mesophyll cell layers and larger amount of photosynthetic apparatus per unit of leaf area (Kull, 2002). However, as this mechanism requires corresponding changes in leaf anatomy, it is fully functional only in developing leaves, and in our results of path analysis (Fig. 3B in II), the indirect positive effect of irradiance on chlorophyll content per unit of leaf area (Chl_a) via increased LMA and N_a, appeared only in deciduous tree canopy, where light conditions measured in July, can be expected to reflect the light availability patterns during leaf development (between the end of April and the beginning of June for the studied tree species). The opposite effect of increased irradiance occurs at the chloroplast level. For the effective use of resources and photoprotection, the relative share of chlorophyll containing light harvesting part compared to the rest of photosynthetic apparatus decreases with increasing light availability. This direct negative effect of irradiance on Chl_a occurs both in young developing leaves and in fully matured leaves (Fig. 3 in II). Given that the re-acclimation of mature leaves to changed light conditions generally does not include the modifications in LMA, it should result in enhanced variability of Chl_a. Indeed, our results showed that one of the striking differences between tree and herbaceous species was that the coefficient of variation of Chl_a was much larger in herbaceous canopy (Table 2 in II). Transfer experiments have also shown that the re-acclimation to modified light environment leads to increased variation in Chl_a (Naidu & DeLucia, 1998; Frak *et al.*, 2001; Oguchi *et al.*, 2003).

Correlations between light availability and leaf nitrogen and chlorophyll contents are used for parameterizing large-scale carbon gain models using remote sensing information (Friend, 2001; Dai *et al.*, 2004), however, as our results (Paper II) showed, modified light environments during vegetation expansion can importantly alter and break down these relationships.

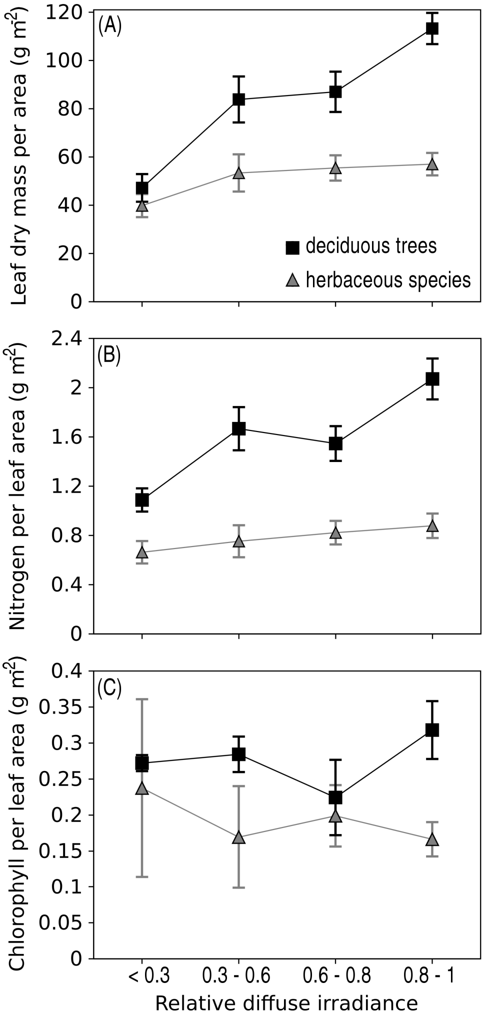

Figure 3. Leaf dry mass (A), nitrogen (B) and chlorophyll (C) content per unit of leaf area, in relation to light availability (measured in July) for deciduous tree and herbaceous species. Error bars denote 95% confidence intervals for mean.

The results of paper II also demonstrated the advantages of deciduous strategy for tree canopies where leaves are formed during a single flush and hence light conditions do not change significantly after leaf maturation. However, it should be remembered that in evergreen tree canopies light availability for a given leaf will also change after leaf maturation (Niinemets, 2007), although the changes are less rapid than in herbaceous canopy. The different strategies for shade tolerance between deciduous and evergreen woody species described in paper I, can partly arise from the different light acclimation capacities of young developing foliage and mature leaves.

Light capture efficiency expressed per foliar nitrogen content and biomass within the herbaceous canopy

In tree canopy, the light environment of a given leaf is largely created by the same tree via self-shading. In herbaceous canopy, there is a great number of individuals and species in close proximity influencing the light regime.

The results of Paper II suggested that changes in leaf light environment due to continuous leaf formation and extension growth in herbaceous canopy, resulted in 'non-optimal' nitrogen distribution along the canopy light gradient, as mature leaves have only a limited capacity to re-acclimate to new light conditions. Comparison of the results from papers I and II could suggest that species growing in fertile conditions, which allow fast growth rates, are forced to have shorter leaf life-spans and quicker leaf turnover to replace old shaded leaves. Therefore, the distribution of light capture efficiency per foliar nitrogen and whole above-ground biomass within herbaceous canopy along soil fertility gradient was further investigated, and the main emphasis was to distinguish between the effect of interspecific plasticity and the importance of different species-specific mean values of the resource-use efficiencies at canopy scale.

Three forb species (*Achillea millefolium* L., *Cirsium arvense* (L.) Scop., *Taraxacum officinale* Weber ex Wigg.) and three grass species (*Dactylis glomerata* L., *Festuca pratensis* Huds. and *Phleum pratense* L.) were present along the entire productivity gradient studied in paper III. These six species produced majority of the biomass (65–95%) in all plots (Fig. 1 in III) and were examined in more detail. Other species were pooled together for analysis as they formed only a minor part of the total biomass and were present only in a few plots. According to Grime (1998) these pooled species belong to the transient species group.

As the changes in species composition were marginal along the productivity gradient, a clear trend was observed in species' biomass proportions. Grasses formed more than 80% of the stand above-ground biomass at the more productive part of the transect, but their relative share declined to less than 50% in less productive sample plots. Forbs had a biomass maximum at medium soil fertility. This raises a question, why some species become dominant when productivity increases, whereas others remain subordinates. The next question would be, how the changes in species composition influence community-level responses as the traits of dominant species should have the major impact determining the functioning of the community (Grime, 1998).

Increasing site fertility usually leads to the decline in available light per unit of leaf area or biomass due to increased LAI and consequently, a decline in light capture per unit of mass can be treated as an indicator of increased competition. Indeed, we found that light absorption per unit of above-ground biomass (Φ_M) decreased significantly with increasing stand biomass (i.e. the stand-level response; Fig. 4 in III) and also for two species at the species level (Fig. 7 in III). However, the stand-level decreasing trend was amplified by a change in relative abundance of species with lower species-specific values of Φ_M with increasing site productivity. For instance the average Φ_M of *P. pratense* and *F. pratensis* was less than that in the other species (Fig. 7 in III). The directionality of light allows dominant species to monopolise this resource more easily than mineral nutrients and therefore, competition asymmetry usually increases in fertile soil (Grime, 1979; Schippers & Kropff, 2001). Competitive asymmetry is also influenced by plasticity of leaf area ratio (LAR), defined as leaf area expressed per plant total biomass (Anten & Hirose, 1998). A striking difference in plasticity of LAR between dominant and subordinate species was revealed in the present study. Grasses, dominating at the more productive plots, had intrinsically low LAR and they responded to increasing soil fertility by reducing LAR even more. In contrast, *A. millefolium* and *T. officinale*, two forb species, increased their LAR in response to intensified competition (Fig. 8 in III). The strategy of dominant species appears to be to overtop others at the cost of reduced LAR, while the strategy of subordinates is to increase light capturing ability by increasing LAR.

The behaviour of light absorption per unit of leaf nitrogen (Φ_N) and above-ground efficiency of nitrogen use (aNUE) at the stand level resulted mainly from changes in relative share of species with different species-specific values. There was almost no dependence of aNUE on site productivity for any species, except a significant decrease in aNUE of *A. millefolium* (Fig. 6 in III), while on the stand level, however, a strong increase in aNUE was revealed along the productivity gradient (Fig. 4 in III). Intrinsically lower tissue nitrogen concentration (i.e. higher aNUE) was a trait characteristic of species which became dominant at high availability of soil resources in our study. As these species had also low LAR, their high aNUE can be at least partly explained by simply greater allocation into nitrogen-poor support tissues (Lemaire & Millard, 1999). Light capture per unit of foliar nitrogen at the species level showed a tendency to decrease with increasing soil fertility (Fig. 5 in III), suggesting that the decreased cost of nitrogen acquisition due to higher soil nitrogen availability was prevailing even in species which showed a tendency to decrease LAR in response to increased competition. The same trend was apparent in less productive plots on the stand level (Fig. 4 in III), however, in the most productive plots the stand-level Φ_N started to increase again. This increase was caused mainly by the growing domination of species, like *P. pratense*, with intrinsically high Φ_N in the more fertile soils.

CONCLUSIONS

Shade conditions are generally created by the surrounding vegetation. The results of this thesis showed complex interactions between phenotypic plasticity and inherent species-specific differences of leaf traits, influencing the ability of plants to cope with limited light conditions. Alternative strategies, which can be partly explained by dynamics of light availability during leaf life-span, were observed among deciduous and evergreen woody species, graminoids and forbs.

(1) In temperate woody flora of the Northern Hemisphere, species shade tolerance was positively related to leaf life-span and negatively related to LMA, N_a and A_a. However, there were also remarkable differences between the functional groups of deciduous broad-leaved species and evergreen conifers, as shade tolerance decreased with A_m within deciduous broad-leaved group and increased within evergreen conifers' group. Although the three functional groups studied here – deciduous broad-leaved, evergreen broad-leaved and evergreen conifers – differ from each other remarkably by leaf longevity, LMA, N_m and A_m, the mean shade tolerance for each group was rather similar, suggesting that along the global gradient of 'leaf economics' the strategy how to achieve shade tolerance varies rather than the shade tolerance itself.

(2) The correlative relationships of leaf structural and chemical traits with respect to current light availability differed between herbaceous and woody species due to contrasting canopy developmental patterns. In the deciduous tree canopy, where new leaf formation mainly occurs in a single flush and leaves experience similar light environment throughout most of their life-span since expansion, LMA and N_a increased significantly with current light availability. In the herbaceous canopy, on the contrary, LMA and N_a were generally not related to current light conditions, reflecting limited re-acclimation potential of mature leaves. Light acclimation of nitrogen content per unit of leaf area was largely mediated by changes in LMA, but the latter is known to be determined by light conditions during leaf development. Increasing light availability had two conflicting influences on leaf chlorophyll content: (I) an indirect positive effect to increase Chl_a due to the growing amount of photosynthetic apparatus, which was mediated by changes in LMA and N_a; (II) the direct negative effect to decrease Chl_a due to the declining amount of light harvesting complexes relative to the rest of the photosynthetic apparatus.

(3) Community-level patterns in light capture, biomass and nitrogen partitioning can be largely attributed to changes in species composition along a productivity gradient in herbaceous stands. Availability of light resource and hence light absorption per unit of biomass (Φ_M) declined with increasing site productivity. Species, which became dominant at high soil resources had lower tissue nitrogen concentrations (high aNUE) and lower LAR, leading to community-level increase in aNUE and decrease in LAR along the productivity gradient. However, some subordinate species increased LAR with increasing soil fertility, indicating that dominant and subordinate species have distinct strategies to cope with increased competition for limited light resource.

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SUMMARY IN ESTONIAN

Valguse neeldumine taimestikus, fotosünteesivõime ja liikide varjutaluvus: üldised seaduspärad ning erinevused funktsionaalsete gruppide vahel

Keskkonnatingimusi, mis ei ole taimede kasvuks optimaalsed, loetakse stressifaktoriteks. Pikem lehe eluiga ning väiksem eripind, väiksem lämmastikusisaldus ja madalam fotosünteesivõime on lehetunnused, mida tavaliselt seostatakse taimede suurema stressitaluvusega. Limiteerivates keskonnatingimustes võimaldavad lehtede pikem eluiga ja väiksem lämmastikusisaldus ning sellest tulenev madalam fotosünteesivõime säästlikumat ressursikasutust. Mehhaaniliselt vastupidavamad lehed on pikaealisemad, kuid suurem tugikudede osatähtsus vähendab lehe eripinda.

Sarnaselt üldise stressitaluvusega võiksid pikem lehe-eluiga ning väiksemad lämmastikusisaldus ja fotosünteesivõime suurendada ka taime varjutaluvust. Lehe suurem eripind parandab aga limiteeritud valgusressursi kasutamise efektiivsust. Uurijate hulgas on üldine konsensus, et sama liigi piires on varjulehtede eripind reeglina suurem kui valguslehtedel. Samas esineb märkimisväärseid lahkarvamusi selles, kas varjutaluvatel liikidel on samades valgustingimustes suurem või väiksem lehe eripind võrreldes valgusnõudlike liikidega.

Lehtede lämmastikusisalduse ja fotosünteesivõime vahelist tugevat seost võib seletada kahe asjaoluga. Seose levinuimaks põhjendus on fakt, et väga suur osa lehes olevast lämmastikust kuulub Rubisco, peamise süsinikku assimileeriva ensüümi, koosseisu. Samas osalevad kõik lehe valgud pidevas energiat nõudvas lagundamise ja taas-sünteesi tsüklis. Seega võib seos lehe lämmastikusisalduse ja fotosünteesivõime vahel tuleneda ka sellest, et leht vajab lämmastiku säilitamiseks ja taastootmiseks teatud hulka fotosünteesist saadavat energiat.

Lämmastikukasutuse efektiivsuseks (NUE) nimetatakse biomassi produktsiooni taime lämmastikusisalduse ühiku kohta. Valgusekasutuse efektiivsuseks (LUE) nimetatakse taime biomassi produktsiooni fotosünteesil neeldunud valgusenergia ühiku kohta. Valguse neeldumist lämmastiku ühiku kohta väljendab NUE/LUE suhe. Kui valgusenergia biomassiks konverteerimine on efektiivsem, siis valguse neeldumine maapealse biomassi ühiku kohta väheneb.

Minu doktoritöö eesmärgiks on uurida, kuidas taimelehtede funktsionaalsed tunnused ning maapealse biomassi jaotus sõltuvad valgustingimustest nii liigisiseselt kui liikide vahel. Otsin vastuseid järgmistele küsimustele:

(1) Kuidas sõltub põhjapoolkera parasvöötme puittaimede varjutaluvus lehtede liigiomasest elueast, eripinnast, lämmastikusisaldusest ja fotosünteesivõimest? Esialgse hüpoteesi kohaselt on suurema varjutaluvusega seotud tunnused, mis suurendavad lehestiku pindala ja vähendavad ressursikulu lehestiku tootmiseks (pikem lehe eluiga, suurem eripind, väiksem lämmastikusisaldus ning madalam fotosünteesivõime).

(2) Kas puit- ja rohttaimedel on erinev seos lehtede klorofülli- ja lämmastikusisalduse ning eripinna vahel piki lehestikusisest vertikaalset valgusgradienti? Eeldasime, et pikaealise võraga puittaimedel on vastavad seosed tugevamad kui rohttaimedel, millede lehtede valgustingimused taimestiku kõrguse kasvades kiiresti muutuvad.

(3) Kas rohttaimede liigispetsiifilised erinevused lämmastikukasutuse efektiivsuses ja maapealse biomassi jaotuses mõjutavad seoseid mullaviljakuse ning taimkattes neeldunud valguse vahel koosluse tasemel? Esialgse hüpoteesi kohaselt on erineva mullaviljakuse tingimustes domineerivatel liikidel erinevad biomassi ja lämmastiku allokatsiooni strateegiad ning need liigiomased erinevused avaldavad mõju funktsionaalsetele seostele koosluse tasemel.

Esimesele küsimusele vastuse leidmiseks kasutasin kirjanduse põhjal koostatud andmebaasi, mis sisaldas andmeid 339 põhjapoolkera parasvöötmes kasvava puuliigi lehetunnuste ja varjutaluvuse kohta. Selles andmebaasis on varjutaluvus defineeritud minimaalsete valgustingimuste kaudu, mille juures antud liik suudab kasvada. Varjutaluvuse väärtus 1 vastab mittetolerantsele liigile, mis vajab kasvamiseks vähemalt 50% täisvalgusest ja varjutaluvuse väärtus 5 tähistab suurimat tolerantsi (liigid mis vajavad 2–5% täisvalgusest). Lehetunnuste (keskmine eluiga, eripind, lämmastikusisaldus ja fotosünteesivõime) liigispetsiifiliste väärtuste arvutamiseks kasutati ainult võra ülemiste, s.t. valguslehtede, andmeid.

Teisele ja kolmandale küsimusele vastamiseks tegin Eestis välimõõtmisi. Järvselja heitlehises segametsas mõõtsime 2000. aasta juulis kolme puuliigi (haab, arukask, harilik pärn) võras erinevatel kõrgustel lehtede klorofülli- ja lämmastikusisaldust ning eripinda. Lehtede valgustingimusi hindasime poolsfäärifotode meetodiga. Elva lähedal Arus mõõtsime 1999. aasta juulis rohttaimi söötijäätud (u. 5 aastat) endisel põllumaal. Sõltuvalt taimkatte kõrgusest jagasime selle vertikaalselt 3–5 kihiks (kihi paksus 15–25 cm). Pealelangeva valguse intensiivsust mõõtsime kvant-sensoriga iga kihi kohal ja all. Igal liigil mõõtsime kõikides kihtides eraldi lehtede kaldenurgad, lehtede mass ja pindala, varte mass ning klorofülli- ja lämmastikusisalduse.

Kirjandusest on teada, et globaalses skaalas varieeruvad liigispetsiifiline lehe keskmine eluiga, eripind, lämmastikusisaldus ja fotosünteesivõime koordineeritult (ingl. k. *leaf economics spectrum*). Minu töö tulemustest selgus, et sama seaduspära kehtib ka põhjapoolkera parasvöötme puittaimedel. Liigid jaotuvad spektril, mis ulatub “ressursisäästlikust” strateegiast (iseloomulikeks tunnusteks on lehtede pikk eluiga, väike eripind, väike lämmastikusisaldus ja madal fotosünteesivõime) kuni kiirekasvuliste liikideni, mille lehtedel on lühike eluiga, suur eripind, suur lämmastikusisaldus ning kõrge fotosünteesivõime. Kirjandusest võib leida väiteid, et ka varjutaluvus on osa üldisest ressursisäästlikust strateegiast ning sellega seletatakse varjutaluvate liikide lehtede madalamat eripinda võrreldes valgusnõudlike liikidega samades valgustingimustes. Minu tulemused näitavad, et põhjapoolkera parasvöötme puittaimedel ei ole liigi varjutaluvus seotud lehetunnustel põhineva üldise ressursisäästliku elustrateegiaga ja varjutaluvamate liikide lehed on küll pikaealisemad, aga samas ka suurema eripinnaga.

Ressursisäästlikkuse kasvamise alusel võib uuritud liigid jaotada järgmisteks gruppideks: heitlehised laialehelised (DB), igihaljad laialehised (EB) ja igihaljad okaspuud (EC). Esimesse gruppi kuuluvad kiirkasvulised liigid ning viimases on ressursisäästliku strateegia esindajad. Kirjanduses on vastukäivaid tulemusi liigi varjutaluvuse ja lehe eripinna vahel püütud põhjendada sellega, et heitlehistel liikidel on see seos positiivne ja igihaljastel liikidel negatiivne. Käesoleva töö tulemused näitavad aga, et põhjapoolkera parasvöötme puittaimede varjutaluvuse ja liigiomase leheeripinna vaheline seos on positiivne ka mõlemas igihaljaste puittaimede grupis (EB ja EC).

Saadud tulemuste põhjal võib öelda, et piki lehetunnuste "ressursisäästlikkuse" gradienti varieeruvad pigem varjutaluvuse saavutamise mehhanismid, mitte varjutolerantsus ise, sest keskmine varjutaluvus ei erine DB, EB ja EC gruppide vahel oluliselt. Küll aga esineb DB ja EC gruppide sees suuri erinevusi üksikute lehetunnuste ja varjutaluvuse vahelistes seostes. Heitlehiste liikide leheeluiga on piiratud kasvuperioodi pikkusega ning nende varjutaluvuse suurendamise strateegiaks näib olevat vähendada ressursikulu lehe pindala- või massiühiku tootmisel, sest DB grupis on varjutaluvuse seos lämmastikusisaldusega (lehe pindalaühiku kohta) ning fotosünteesivõimega (nii pindala- kui massi ühiku kohta) negatiivne. Igihaljastel okaspuudel on pikim lehtede eluiga ning ka seos leheeluea ja varjutaluvuse vahel on selles grupis tugevaim. Vastupidiselt heitlehistele liikidele on igihaljaste okaspuude grupis varjutaluvuse seosed lehe fotosünteesivõimega (massiühiku kohta) ja fotosünteesi lämmastikukasutuse efektiivsusega (fotosünteesivõime lämmastikusisalduse ühiku kohta) positiivsed.

Lisaks liigispetsiifilistele erinevustele varieeruvad lehe tunnused sama liigi piires ka valgus- ja varjulehtedel. Uurisin, kuidas on heitlehiste puit- ja rohttaimede lehestikus klorofülli- ja lämmastikusisaldus ning eripind seotud vertikaalse valgusgradiendiga. Puittaimede varjulehtedel oli võrreldes valguslehtedega suurem eripind ja väiksem lämmastikusisaldus lehe pindalaühiku kohta. Rohttaimedel puudus üldjuhul seos nende lehetunnuste ja valgustingimuste vahel. Rohttaimedel moodustuvad reeglina pidevalt uued lehed lehestiku ülemises osas hea valguse kättesaadavuse tingimustes, mis jäävad hiljem, taime kõrguse kasvades, varju. Pikaealise võraga heitlehistel puittaimedel, mille peamine lehtede produktsioon toimub kevadel, kasvuperioodi alguses, muutuvad valgustingimused lehe eluea jooksul märksa vähem ning suurem osa valgustingimuste muutustest toimub enne lehe täiskasvanuks saamist. Kuna täiskasvanud lehed eripinda märkimisväärselt muuta ei saa, seletab see valgustingimuste dünaamika erinevus seose puudumist rohttaimede lehtede eripinna ning valgustingimuste vahel. Seos valgustingimuste ning lehe lämmastikusisalduse (väljendatuna pindalaühiku kohta) vahel sõltub peamiselt lehe eripinnast. Täiskasvanud lehtede klorofüllisisaldus võib vastavalt muutunud valgustingimustele märkimisväärselt muutuda. Minu tulemused (teeanalüüs, ingl. k. *path analysis*) näitavad valgustingimuste kahte vastandlikku mõju lehe klorofüllisisaldusele. Valguse parem kättesaadavus tingib läbi lehtede eripinna ning lämmastikusisalduse muutuste suurema klorofüllisisalduse, sest suureneb kogu fotosünteesiaparaat (kaudne positiivne mõju). Samas on valgusel klorofülli hulgale ka otsene negatiivne mõju: klorofülli osakaal fotosünteesiaparaadis väheneb, sest tugeva valguse tingimustes võimaldab väiksem pigmendi kogus samas hulgas valguseenergiat siduda.

Uurides niidukoosluses valguse neeldumist biomassi ja lämmastikusisalduse ühiku kohta, leidsin, et erineva mullaviljakuse juures domineerivate liikide tunnused mõjutasid oluliselt koosluse tasemel seoseid. Kõrgema mullaviljakuse korral vähenes valguse neeldumine biomassiühiku kohta, sest vähenes ka pealelangeva valguse hulk biomassiühiku kohta. Kõrge mullaviljakuse korral domineerivad liigid olid suurema lämmastikukasutuse efektiivsuse (maapealse biomassi kogus lehelämmastiku ühiku kohta) ning väiksema lehepinna suhega (lehtede pindala maapealse biomassi ühiku kohta). Seetõttu suurenes mullaviljakuse tõustes koosluse tasemel lämmastikukasutuse efektiivsus ning vähenes lehepinna suhe. Siiski esines ka teistsuguse strateegiaga liike, millel mullaviljakuse tõustes lehtede pindala maapealse biomassi ühiku kohta suurenes.

Antud töö tulemuste põhjal võib kokkuvõtteks öelda, et (1) põhjapoolkera parasvöötme puittaimedel on varjutaluvus üldiselt liigispetsiifilise keskmise lehe eluea ja eripinnaga positiivses seoses ning lämmastikusisalduse ja fotosünteesivõimega (väljendatuna pindalaühiku kohta) negatiivses seoses, kuid funktsionaalsete gruppide siseselt esineb seostes üksikute lehe tunnustega märkimisväärseid erinevusi; (2) puittaimedel on seosed lehetunnuste (eripind ning klorofülli- ja lämmastikusisaldus) ja valgustingimuste vahel piki lehestikusisest vertikaalset valgusgradienti tugevamad kui rohttaimedel ning (3) rohttaimede lämmastikukasutuse efektiivsuse ja maapealse biomassi jaotuse liigiomased erinevused mõjutavad oluliselt koosluse-tasemel avalduvaid seoseid taimkattes neeldunud valgusega.

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