

ANNE AAN

Light- and nitrogen-use and biomass
allocation along productivity gradients
in multilayer plant communities



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CONTENTS

LIST OF ORIGINAL PUBLICATIONS	6
LIST OF ABBREVIATIONS	7
1. INTRODUCTION	8
2. MATERIALS AND METHODS.....	11
2.1. Site characteristics.....	11
2.2. Soil sampling (III, IV).....	12
2.3. Light measurements	12
2.4. Biomass and foliage measurements	13
2.5. Determination of nitrogen and chlorophyll concentrations	14
2.6. Statistical analysis	14
3. RESULTS	16
3.1. Two-resource model (I).....	16
3.2. What may give an advantage to graminoids as compared to forbs with increasing site productivity? (II)	16
3.3. Description of productivity gradients (III, IV).....	17
3.4. Aboveground biomass allocation patterns and asymmetry of competition	18
3.5. Nitrogen-use efficiency (NUE)	20
3.6. Light-use indices and partitioning of light	21
3.7. Trade-off between leaf area ratio (LAR) and nitrogen content per leaf area (N_A).....	22
3.8. Dominants versus subordinates	22
4. DISCUSSION.....	23
4.1. Two-resource model (I).....	23
4.2. What may give an advantage to graminoids as compared to forbs with increasing site productivity? (II)	24
4.3. Aboveground biomass allocation patterns and asymmetry of competition	25
4.4. Nitrogen-use efficiency (NUE)	26
4.5. Light-use indices and partitioning of light	27
4.6. Trade-off in light- and nitrogen-use	28
4.7. Dominants versus subordinates	28
5. CONCLUSIONS	30
REFERENCES.....	32
SUMMARY IN ESTONIAN	36
ACKNOWLEDGEMENTS/TÄNUSÕNAD.....	40
PUBLICATIONS	41
<i>CURRICULUM VITAE</i>	112

LIST OF ORIGINAL PUBLICATIONS

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

- I Kull O, Aan A, Sõelsepp T. 1995. Light interception, nitrogen and leaf mass distribution in a multilayer plant community. *Functional Ecology* **9**: 589–595.
- II Kull O, Aan A. 1997. Relative share of graminoid and forb life forms in natural gradient of herb layer productivity. *Ecography* **20**: 146–154.
- 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.
- IV Aan A, Lõhmus K, Sellin A, Kull O. (submitted). Changes in light- and nitrogen-use and in aboveground biomass allocation patterns along productivity gradients in grasslands. *Journal of Vegetation Science*.

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The participation of the author in preparing the listed publications is as follows:
paper I – collecting data (80%), analysing data and preparing the text (20%);
paper II – collecting data (90%), analysing data and preparing the text (30%);
paper III – collecting data (90%), analysing data and preparing the text (60%);
paper IV – collecting data (100%), analysing data and preparing the text (90%).

LIST OF ABBREVIATIONS

aNUE	aboveground nitrogen-use efficiency, calculated as aboveground plant dry mass per unit of total leaf nitrogen ($\text{g g}^{-1} \text{N}$)
<i>B</i>	parameter of competition asymmetry
LAI	leaf area index, calculated as leaf area per unit ground area ($\text{m}^2 \text{m}^{-2}$)
LAR	leaf area ratio, calculated as leaf area per unit of aboveground dry mass ($\text{m}^2 \text{kg}^{-1}$)
LMA	leaf dry mass per unit leaf area (g m^{-2})
LMF	leaf mass fraction, calculated as leaf dry mass per unit of aboveground dry mass ($\text{g leaf g}^{-1} \text{plant}$)
LUE	light-use efficiency, defined as plant productivity per unit of absorbed light (g mol^{-1})
<i>M</i>	aboveground dry mass (g m^{-2})
N_A	foliar nitrogen content per unit leaf area (g m^{-2})
N_L	foliar nitrogen content per unit ground area (g m^{-2})
NUE	nitrogen-use efficiency, defined as productivity per unit of plant nitrogen content ($\text{g g}^{-1} \text{N}$)
<i>P</i>	net photosynthesis ($\text{mol CO}_2 \text{m}^{-2} \text{day}^{-1}$)
PPFD	photosynthetic photon flux density ($\text{mol photons m}^{-2} \text{day}^{-1}$)
Φ	absorbed photons ($\text{mol m}^{-2} \text{day}^{-1}$)
SLA	specific leaf area, calculated as leaf area per unit of leaf dry mass ($\text{m}^2 \text{kg}^{-1}$)
Φ_M	light absorption per unit of aboveground mass ($\text{mol g}^{-1} \text{day}^{-1}$ or $\text{g}^{-1} \text{DM}$)
Φ_N	light absorption per unit of leaf nitrogen ($\text{mol g}^{-1} \text{N day}^{-1}$ or $\text{g}^{-1} \text{N}$)

I. INTRODUCTION

Plants need various resources in sufficient quantities for their growth, successful reproduction and survival. The levels of available resources are not equal for different canopy layers in a multilayer plant community, especially on the occasion of light (Valladares 2003; Niinemets 2007). Shading and light interception in the community generate a vertical gradient, where the uppermost layer (usually tree layer) receives the highest amount of photons, but the ground layer (generally moss layer) receives the lowest irradiance.

One of the possible explanations for species coexistence proceeds from the different ability of plant species to acquire and use different resources. Light and nitrogen availability are two of the factors limiting plant growth in natural communities most frequently (Tilman 1988). Consequently, it is vital that light and nitrogen resources are efficiently utilized by plants. Reich (2012) found that stand-scale productivity of forests is a function of LAI (capacity to harvest light) and canopy nitrogen concentration reflecting potential to fix carbon biochemically. Nitrogen acquisition is an expensive process in terms of carbon costs for plants and accordingly the quantity of nitrogen that is allocated to leaves is limited (Anten et al. 2000). Water availability is crucial for plant functioning and survival as well (Kozlowski and Pallardy 2002; Chaves et al. 2003; Duan et al. 2005), but I do not examine this issue in more detail in my studies.

Understanding of the relationships between biomass allocation, light interception and competition is essential to describe the contribution of individual plant species to vegetation structure (Anten and Hirose 1998). Hirose and Werger (1994, 1995) invented an analysis of light flux partitioning between species in the canopy. They evaluated photon absorption per unit of biomass (Φ_M) and photon absorption per unit of leaf nitrogen (Φ_N) in dominant (overstory) and subordinate (understory) species in the same soil conditions. Although tall species intercepted 75% of incident light, Φ_M of dominants was not higher compared to subordinates. They concluded that the efficiency of aboveground biomass to acquire light is a compromise between large leaf area ratio (LAR) + remaining in shade, and increased stem length that enables plants to position leaves into better-illuminated area + lower LAR and consequently reduced efficiency (Hirose and Werger 1995). Kamiyama et al. (2010) suggest that Φ_M , i.e. light acquisition efficiency, is a valuable indicator of species strategy for photon absorption. Parameter Φ_N reflects the potential carbon fixation rate per unit of leaf nitrogen. Hirose and Werger (1994) found that Φ_N does not differ between dominants and subordinates in the community.

Plant C economy is co-determined by the rate of photosynthesis and respiration and LAR (Poorter et al. 2012). A high stand-level LAR means a large photosynthesizing surface that ensures great light absorption and consequently higher CO₂ fixation capacity. On the other hand, if stand density is high, plants have to form longer stems (i.e., to enlarge allocation into supporting structures) to project the foliage into better-illuminated environment. Thus, one can distinguish between two allocational or structural strategies: to invest either more

to leaves or to stems in order to overtop neighbours and achieve greater light interception. LAR may be divided into two components: specific leaf area (SLA) and leaf mass fraction (LMF). SLA is a quantity depending on leaf morphology, but LMF shows biomass allocation to leaves relative to other plant organs. Consequently, it is essential to examine which component of LAR varies more, because LAR indicates surface of leaf area per unit of plant biomass. Poorter et al. (2009, 2012) concluded that inherent differences in SLA are much larger than those in LMF.

Plants should have high nitrogen uptake rate or high nitrogen-use efficiency (NUE) or both (Chiba and Hirose 1993) to support high growth rates in a nitrogen-limited environment. There exist various definitions of nitrogen-use efficiency, depending on time scale and organisation level, e.g. as a rate of photosynthesis per unit of leaf nitrogen content (Hirose 1984; Field and Mooney 1986). On a longer time scale, it is calculated as a biomass increment per unit of nitrogen taken up (Vitousek 1982; Rundel 1982). At present, Hirose (2012) distinguishes leaf-, plant- and stand-level NUE. He suggests that examining NUE at lower levels helps to understand N economy in different species and in communities growing along nutrient availability gradients. Using an inverse of tissue N concentration as a rough estimate of NUE has been used in several papers (Chapin 1980; Shaver and Melillo 1984; Schimel et al. 1991). On the other hand, it is important to distinguish between the two components of NUE for more precise study: 1) instantaneous nitrogen productivity and 2) mean residence time of N in the plant (Berendse and Aerts 1987).

Light partitioning analysis has enabled researchers to demonstrate an inverse relationship between plant stand nitrogen- and light-use efficiencies (Hirose and Bazzaz 1998). Hirose and Bazzaz (1998) defined light-use efficiency as the ratio of net photosynthesis to absorbed photosynthetically active radiation (i.e. $LUE = P/\Phi$), and nitrogen-use efficiency as the ratio of net photosynthesis to leaf nitrogen content ($NUE = P/N$). Consequently, the light absorption per unit of nitrogen equals the ratio of NUE to LUE ($\Phi_N = NUE/LUE$). If aboveground nitrogen-use efficiency, aNUE, is defined as the ratio of aboveground biomass per foliar nitrogen content (i.e. $aNUE = M/N_L = \Phi_N/\Phi_M$), and if aNUE is assumed to be proportional to total NUE, then Φ_M should be proportional to $1/LUE$. Consequently, as LUE is expected to increase along a productivity gradient, Φ_M should decline. In general, plants have to compromise between effective light-use, nitrogen-use and biomass allocation to better accomplish one of these resource uses.

Werger et al. (2002) observed species replacement and light resource use after cessation of grazing on grasslands. Their data showed that plants react differently to changes in competition caused by increased stand productivity, and that species replacement can be explained by differences in inherent constraints on the shoot architecture in various species. Accordingly, the above-mentioned authors examined plant responses in similar conditions or successional series. However, there is still little information on species replacement

and their light- and nitrogen-use characteristics on a spatial scale. Natural productivity gradient in a plant community offers a wide range of combinations of various abiotic conditions and inter- and intraspecific competition differing in intensity. Moreover, productivity gradient enables examination of plasticity, responses of plant species in their natural environment.

In the present PhD thesis the following hypotheses were proposed:

- 1) Inasmuch as light and nitrogen are two essential resources for plant functioning and growth, they are accordingly important determinants of aboveground biomass of vegetation layers. Therefore, the development of a two-resource model can broaden our understanding of the mechanisms determining productivity of plant communities.
- 2) Light acquisition efficiency (light absorption per unit of biomass) decreases with rising community productivity.
- 3) Aboveground nitrogen-use efficiency diminishes with increasing site productivity.
- 4) A decrease in leaf area ratio is a universal response to increasing aboveground biomass in herbaceous communities.
- 5) Species have distinct properties to cope with various environmental conditions. Subordinate species have morphological/functional traits which enable them to grow under the shade of dominants.

In order to test the hypotheses the following aims were set up:

- 1) To analyse light interception, nitrogen and leaf mass distribution in different layers of several plant communities: from open temperate grassland to wooded meadow and deciduous forest stand. Furthermore, we developed a model to describe vertical distribution of foliage mass in a community as a function of available nitrogen and light. (I)
- 2) To apply the approach of Hirose and Werger (1995) of light partitioning in an herbaceous canopy along natural productivity gradients and to compare response patterns of light-use indices at a community level and in more abundant species. (III, IV)
- 3) To assess nitrogen-use efficiency (NUE) at the community level and in different growth-forms and species along productivity gradients of grasslands (I–IV).
- 4) To reveal whether a decrease in leaf area ratio (LAR) is the universal response to increasing aboveground biomass in herbaceous communities; more specifically, what is responsible of the change in LAR, specific leaf area (SLA) or leaf mass fraction (LMF)?
- 5) To compare light capturing ability and NUE in different herbaceous communities with respect to their structural properties; moreover, to clarify which properties give an advantage to dominants and which enable subordinates to cope and survive under dominant species (III–IV).
- 6) To examine whether there is a trade-off between LAR and foliar nitrogen content per leaf area, N_A (III–IV).

2. MATERIALS AND METHODS

2.1. Site characteristics

Most study areas are located at Laelatu (58°35' N, 23°34' E) (Fig. 1) in western Estonia, on the eastern coast of the Baltic Sea (papers I–II and IV). The mean temperature in July is 17°C, and in January –5°C. The mean annual precipitation is ~500 mm. The soil is mainly a Rendzic Leptosol with a pH around 7. The parent material is limestone shingle mixed with various coastal sediments. The overstory, where present, is species-rich, consisting of *Quercus robur* L., *Betula pendula* Roth, *Fraxinus excelsior* L., *Populus tremula* L., *Pinus sylvestris* L., *Juniperus communis* L., *Corylus avellana* L., *Cornus sanguinea* L., *Viburnum opulus* L. among others. The herb layer consists mainly of perennial forbs and grasses, and is extremely species-rich. Up to 63 vascular plant species per 1 m² have been counted in some parts of the study area (Kull and Zobel 1991).

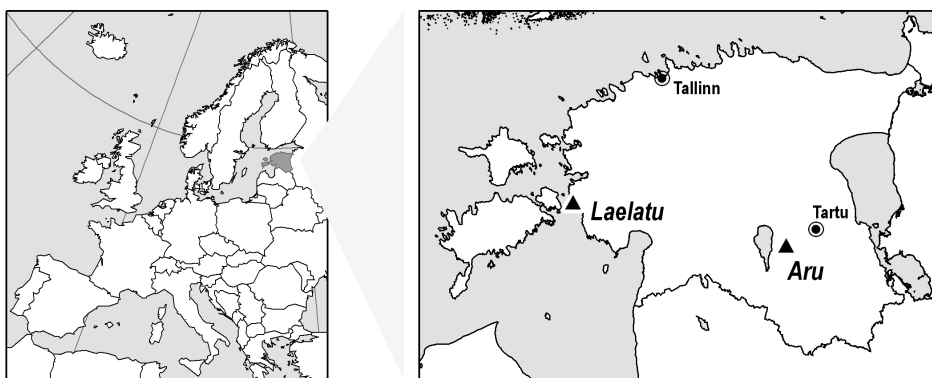


Figure 1. Map and location of the study areas at Laelatu and Aru.

In study I, three vegetation layers (tree, herbaceous and moss layers) were examined along a productivity gradient from open meadow through wooded meadow to closed broad-leaved forest. In paper II, only the herb layer was investigated in 21 sample plots.

Study IV was performed in an almost open meadow, in which two herb layer transects along productivity gradients were selected for examination. The first community (W) is dominated solely by one grass species *Molinia caerulea* (L.) Moench. The wet and more productive part of the site is represented by *Tetragonolobo-Molinietum* association (Krall et al. 1980); the dryer and less productive is covered by *Primulo-Seslerietum* vegetation. Three species: forb *Filipendula ulmaria* (L.) Maxim. and grasses *Elymus repens* (L.) Gould and *Brachypodium pinnatum* (L.) P. Beauv. dominate the second community (D).

The moist and productive part of the site belongs to a *Molinio-Cnidietum* community, the dry and less productive to *Seslerio-Filipenduletum*. The soil water status in W site ranged from very moist (the groundwater table was close to the soil surface, approximately at 20 cm depth) to moderately moist. In D site, there was a gradient from moderately moist to dry soil (Table 1 in III). Its soil texture was sandier compared to the soil in W, where the texture was more clayey. Lower litter quality and too wet soil conditions refer to a slower nitrogen cycle in site W. Although there was higher soil nitrogen concentration compared to that of D site, both plant leaves and litter layer had lower nitrogen concentrations than those in D site (Tables 1 and 2 in III). Soil varies from Salic Gleysol to Rendzic Gleysol (classified by WRB) in W site and from Gleysol to Rendzic Leptosols on coastal deposits in D site. Eight sample plots were distributed along a productivity gradient of herbaceous stand in W site and 10 sample plots were distributed in D study area.

The study area of paper III was situated at Aru (58°16' N, 26°20' E) (Fig. 1) near Tartu in southern Estonia. Ten 1 × 1 m plots were distributed in an old grassland along the slope of a small hillock that created a gradient in soil fertility conditions.

2.2. Soil sampling (III, IV)

One composite sample of soil from the A horizon was taken for analysis from each sample plot. Additionally, a small pit was excavated to measure the thickness of the A horizon and to take samples for bulk density analysis. The soil moisture content was determined by the difference in weight between the fresh and dried samples (III).

In the fourth paper, the soil samples were collected to determine soil moisture and nitrogen contents. Nitrogen concentration of soil samples in both studies (III–IV) was measured by the Kjeldahl method with a Kjeltac Auto 1030 analyser (Tecator, Sweden).

2.3. Light measurements

Herb (I–IV) and moss (I) layers were examined and harvested from 0.5 × 0.5 m plots. In paper III, light measurements were performed in 1 × 1 m plots.

In studies I–II, all field measurements were carried out in July 1991. Three canopy layers under investigation were: tree+shrub, herb and moss layers. Light interception by the tree+shrub layer was estimated by the hemispherical photographic technique (Anderson 1964; improved by Bréda et al. 2002). Light intensity in the herb layer was measured with a 30 cm long specially designed line-sensor pyranometer. The mean interception was calculated from five measurements of irradiance above and below the herb layer. Light interception by the

moss layer was calculated on the assumption that all light penetrating the upper layers was intercepted by the mosses. In paper II, the herb layer was divided into two strata. Vertical division of the layer was made according to the height of half light interception.

In paper III, the field studies were carried out in July 1999. The herbaceous community was vertically divided into 3–5 layers each 15–25 cm thick (depending on stand height). The division was performed to show the vertical distribution of different species: dominants and subordinates. The actual profile of photosynthetic photon flux density was measured with an LI-185B quantum meter equipped with an LI-191SB line quantum sensor (Li-Cor, Nebraska, USA).

In paper IV, the field investigations were made in July 1996. Light interception in the herbaceous community was measured with a 30-cm line-sensor pyranometer. The herbaceous stand was divided into 3 or 4 layers depending on stand height. The interception was calculated from the average of five measurements above and below each herb layer. Light absorption partitioning between species was calculated in studies III and IV; the formulae are given in the respective papers.

In studies III–IV, asymmetry of light competition (B) was calculated from the equation by Anten and Hirose (1998):

$$\Phi_j = c \times (M_j)^B$$

where Φ_j is the total absorbed light, M_j is the total aboveground dry mass of species j , and c is a constant. The value of B was calculated for each plot from simple linear regression of log-transformed values of Φ_j and M_j .

2.4. Biomass and foliage measurements

In study I, the leaf canopy was divided into three layers at every sample point: trees and shrubs, herbaceous plants, and mosses. Foliar dry mass of the tree+shrub layer was calculated indirectly using light interception data and leaf samples. Leaf area index was transformed into canopy leaf mass per area using the values of average leaf dry mass per area (LMA). Moss layer was harvested from the plots and all green parts of the mosses were considered as foliage.

In papers I–IV, all the aboveground parts of the herbaceous community were harvested from each sample plot. Herbaceous plants were sorted into two compartments: leaves and stems + generative organs. In paper II, the herb layer was collected from sample plot by two canopy layers. Vertical separation of the layers was made according to the height of the half light interception. Species were identified for both layers separately and herbs of both layers were sorted into two growth-forms – forbs and graminoids. In study III, the canopy was

harvested from the sample plots by 3 to 5 vertical layers depending on canopy height. The fresh mass of each fraction was measured immediately after sorting.

In paper IV, the aboveground parts of the plants were harvested from the plots by 3 or 4 layers depending on canopy height. Species composition was identified. Foliar samples of more abundant species from each harvested canopy layer were taken for leaf area determination. Images of the air-dried leaves were digitised and projected leaf areas calculated with an in-house computer program PINDALA (A. Kalamees). The leaves were then dried at 80°C to constant weight and specific leaf area (SLA) was calculated. Thereafter, dry mass data of leaves from each sampled canopy layer were used to calculate the total leaf area of separate species in each canopy layer.

In studies I–IV, all the sorted plant material was dried at 80°C to constant weight and dry mass was determined.

2.5. Determination of nitrogen and chlorophyll concentrations

Nitrogen concentration was measured by the Kjeldahl method with a Kjeltac Auto 1030 analyser (Tecator, Sweden) as follows:

Paper I – in the leaves of trees and herbs and in the living parts of the mosses;

Paper II – in the leaves of forbs and graminoids for two strata separately;

Papers III–IV – in the leaves of separate layers of plant species.

In study III, chlorophyll concentration in plant leaves was determined in 80% aqueous acetone with a PS2000 spectrometer (Ocean Optics, USA) following the method by Porra *et al.* (1989).

Chlorophyll (for paper III) and nitrogen concentrations were analysed in all species that had sufficient amount of foliage material within a sampled canopy layer.

2.6. Statistical analysis

In paper I–II, data were analysed with the statistical analysis package STATGRAPHICS (STSC Inc. 1987). In the first study the effect of layer was analysed by one-way ANOVA and intercepted light was taken as a covariate. In study II, two-way ANOVA was used to evaluate productivity (two levels: $<175 \text{ g m}^{-2}$ of foliage, 11 sample plots; $\geq 175 \text{ g m}^{-2}$ of foliage, 10 sample plots), life-form (forb or graminoid) and productivity $\times$ life-form interaction effects on the vertical distribution of foliage and foliar nitrogen. The least-square linear regression technique was used to fit the relationships.

In studies III–IV, statistical analysis was performed using STATISTICA software (StatSoft Inc. USA). For the calculations in paper III, no data transfor-

mation was necessary. Pearson's correlation coefficients were calculated for the analysis of soil and vegetation parameters, General Linear Models (GLM) procedure was used for the regression analysis in paper III.

In paper IV, GLM procedure was used for the regression analysis. Logarithmic or quadratic transformations of data were performed if a deviance from normal distribution occurred. Pearson's correlation coefficients were calculated between soil characteristics and vegetation parameters. Characteristics of the species occurring at both areas were compared by *t*-test for independent groups. Multiple regression analysis was performed to estimate the relationship between aboveground biomass and soil factors: soil moisture and nitrogen concentration. Nonlinear relationships were found with the help of SIGMAPLOT software for Windows (SPSS Inc. 2001).

In all papers adjusted R^2 (denoted as R^2) was used to describe the strength of the relationships.

3. RESULTS

3.1. Two-resource model (I)

The vertical structure of a multilayer plant community ranging from open meadow to broad-leaved forest at Laelatu site was described using a two-resource model. We developed a simple model with a minimum number of parameters in order to describe foliage dry mass distribution among different layers in a community as a function of available soil nitrogen and light (Fig. 1 in I and model description in I). Multiple regression analysis showed that biomass of the layer is determined by relative irradiance above the layer and by the amount of nitrogen in the N cycle. Consequently, general model predictions were consistent with empirical data.

Total foliage dry mass increased with increasing amounts of total foliar nitrogen (Fig. 2 in I). Also, the contribution of the moss layer to total canopy dry mass was higher at low nitrogen availability, whereas the proportion of nitrogen in the tree canopy was larger at higher total canopy nitrogen amounts. The amount of nitrogen increased more rapidly than light interception with increasing site productivity due to denser tree canopy layers (Fig. 3 in I). At low light interception values, the herbaceous layer tended to have more nitrogen per unit ground area than the other layers (Table 2 in I).

The ratio of dry mass to nitrogen varied most in the moss layer, whereas it remained almost constant in the tree canopy layer and changed little in the herb layer (Fig. 5 in I).

3.2. What may give an advantage to graminoids as compared to forbs with increasing site productivity? (II)

Graminoids became dominant in highly productive and well-illuminated habitats of the wooded meadow at Laelatu site. The dominance of graminoids appeared both in terms of leaf mass proportion and species number (Fig. 5 and 6 in II). Total species number decreased with increasing productivity in the herbaceous layer, because of the decrease in forb species number.

Foliage dry mass of graminoids steadily increased with rising herbaceous layer productivity, whereas foliage mass of forbs had a maximum at intermediate values of the total herbaceous foliar mass (Fig. 6. in II). The different behaviour of two growth-forms in a productivity gradient was statistically significant (Table 1 in II). Graminoid species did not have statistically ($P>0.05$) higher canopy compared to forb species (Table 2 in II).

Nitrogen concentration in graminoid foliage was ~20% lower than in forbs (Table 2 in II). Average aboveground nitrogen-use efficiency (aNUE) of forbs was $74.5 \text{ g g}^{-1} \text{ N}$ and in graminoids $85.4 \text{ g g}^{-1} \text{ N}$ (t -test for dependent samples,

$P=0.045$). Figure 2 shows the tendency for the difference in aNUE between the two growth-form groups to increase with rising incident light. The respective relationship with aNUE was statistically stronger than with foliage dry mass to leaf nitrogen ratio (DM_L/N ; Fig. 7 in II).

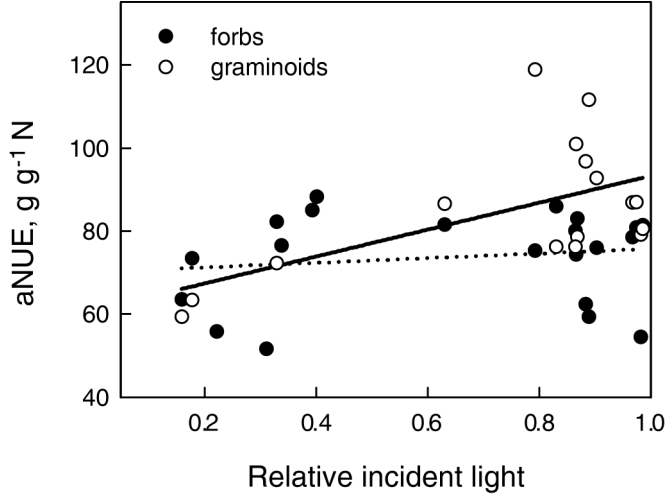


Figure 2. Relationship between relative incident light (measured as a proportion of full light) and aboveground nitrogen-use efficiency (aNUE) in forbs (n.s.) and graminoids ($R^2=0.274$, $P=0.022$).

3.3. Description of productivity gradients (III, IV)

Previous studies have revealed the necessity to increase the number of vertical layers (≥ 3) in the herb community to study light- and nitrogen-use indices and biomass allocation patterns more thoroughly. Three grasslands located at Aru and Laelatu sites were chosen to examine the behaviour of light and nitrogen resource-use indices in more detail along transects representing a productivity gradient. One high-LAR and two low-LAR communities were investigated in papers III and IV.

In study III, slope of the landscape (approximate angle 5°) resulted in a clear gradient in soil conditions, the most apparent of which is the decreasing thickness of the humus horizon from the bottom to the top of the hillock (Table 1 in III). This profile caused a gradient in aboveground biomass ranging from 150 to 490 g m^{-2} (Table 1 in III). Six species, *Achillea millefolium* L., *Cirsium arvense* (L.) Scop., *Taraxacum officinale* Webb, *Dactylis glomerata* L., *Festuca pratensis* Huds. and *Phleum pratense* L., produced most of the biomass (65–95%) in all plots and were present along the entire gradient (Fig. 1 in III). Grasses (mainly *D. glomerata* and *P. pratense*) formed less than 50% of the stand biomass at the less productive part of the gradient and increased to more than 80% in the more productive areas of the gradient (Fig. 1 in III). Forbs (*A. mille-*

folium, *C. arvense* and *T. officinale*) exhibited maximum biomass in the middle of the gradient and it declined in more productive part due to competition with grasses.

In paper IV, the first community (wet, W) was characterized by a smaller productivity gradient, in which the aboveground biomass ranged from 341 to 503 g m⁻². It was dominated by one species, *Molinia caerulea*. The other community (dry, D) exhibited a biomass gradient from 248 to 682 g m⁻² and it had several dominant species: *Filipendula ulmaria*, *Elymus repens*, *Brachypodium pinnatum*, which replaced each other along the gradient. Biomass gradients were driven both by soil moisture and nitrogen shifts along the transects.

3.4. Aboveground biomass allocation patterns and asymmetry of competition

Community-level leaf area ratio (LAR) decreased at Aru (Fig. 3a), while it increased in Laelatu W stand and had a tendency to decrease in Laelatu D site (Fig. 3a). In analysing the components of LAR, the herb layer at Aru showed remarkable change both in specific leaf area (SLA) and leaf mass fraction (LMF). SLA increased and LMF decreased along the productivity gradient (Figs. 3b and 3c). The increase in SLA of the W herb stand in Laelatu was responsible for the change in community-level LAR (Fig. 3b). By contrast, decrease in biomass allocation to leaves (LMF) in D community caused the diminishing trend of LAR (Fig. 3c).

The relative gain in light absorption of a species from increasing biomass depended clearly on site productivity and total leaf area index (LAI), because the asymmetry of competition (parameter *B*) increased with increasing stand total LAI (Fig. 2 in III). This implies that asymmetry of competition increased with increasing stand biomass, inasmuch as species benefit from the relative increase in domination disproportionately with light capturing ability.

In study IV, light competition was more asymmetric (parameter *B* had greater values) in the monodominant community characterised by higher LAI and LAR in site W compared to site D with lower LAI and LAR (Table 2 in IV).

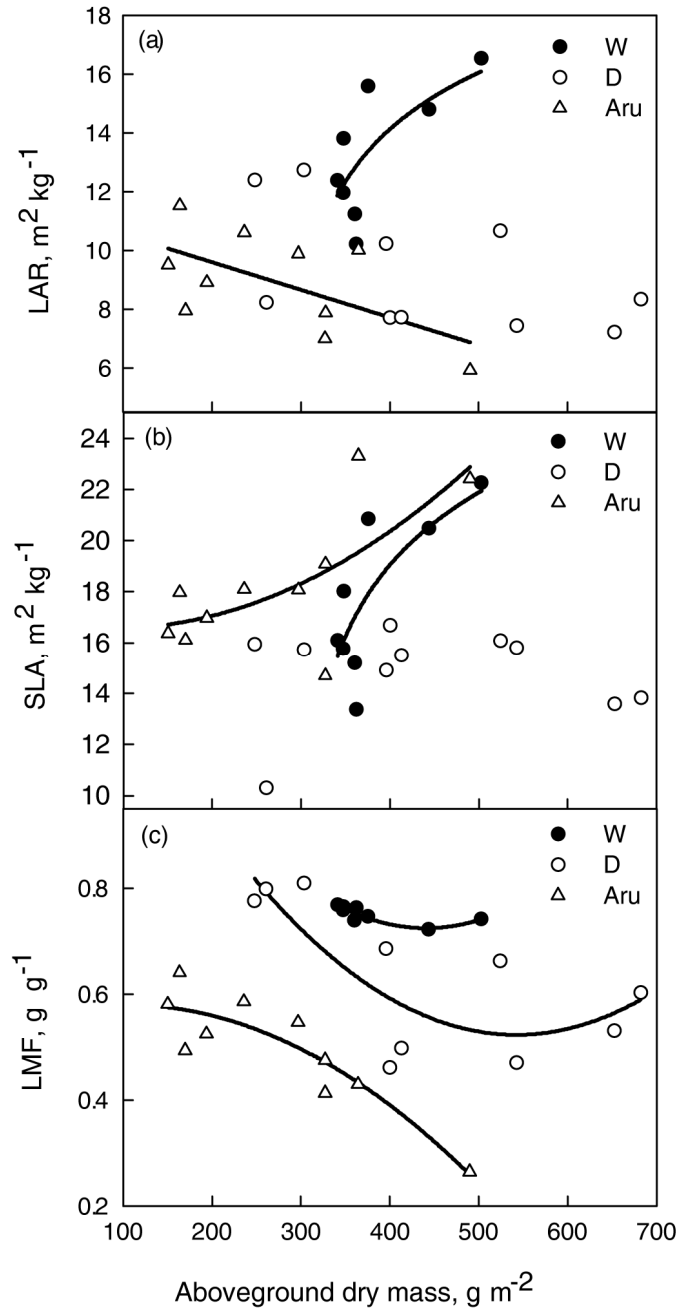


Figure 3. Relationship between aboveground dry mass and community-level (a) leaf area ratio (LAR) in Laelatu W site ($R^2=0.407$, $P=0.053$) and Aru site ($R^2=0.272$, $P=0.070$); (b) specific leaf area (SLA) in Laelatu W site ($R^2=0.503$, $P=0.030$) and Aru site ($R^2=0.344$, $P=0.095$); (c) leaf mass fraction (LMF) in Laelatu W site ($R^2=0.714$, $P=0.019$), Laelatu D site ($R^2=0.501$, $P=0.037$) and Aru site ($R^2=0.758$, $P=0.003$).

3.5. Nitrogen-use efficiency (NUE)

Aboveground nitrogen-use efficiency (aNUE) showed a clear increase with the rise in productivity (Figs. 4a and 4c in III) in Aru site. aNUE diminished in the monodominant and high-LAR community. It increased in central part of the gradient in D site, where low-LAR graminoids dominate (Fig. 4a). aNUE decreased with increasing productivity in the monodominant community

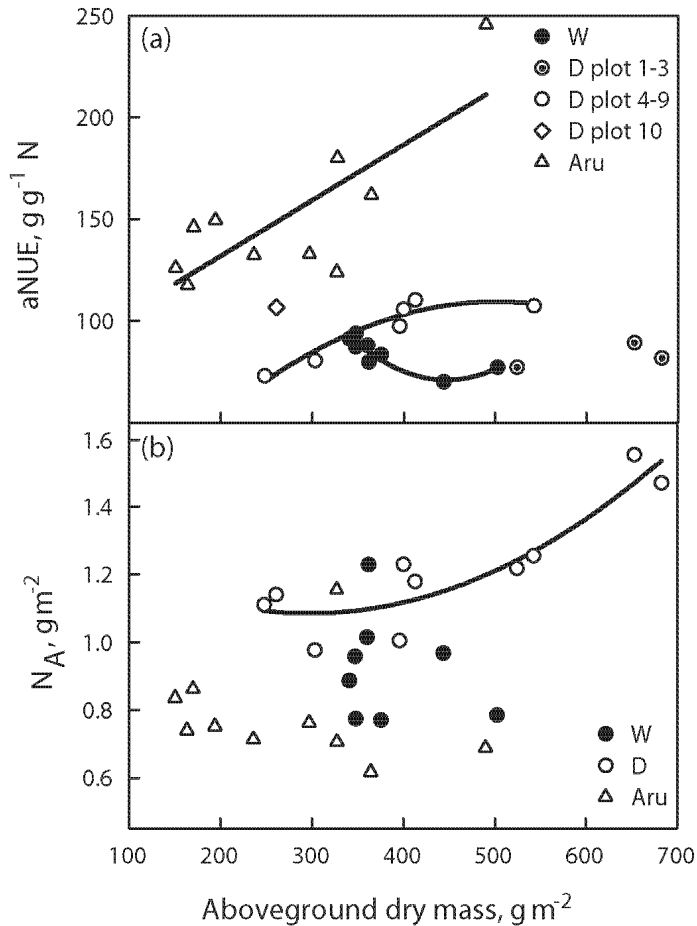


Figure 4. Relationships between aboveground dry mass and community-level (a) aboveground nitrogen-use efficiency (aNUE) in Laelatu W site ($R^2=0.802$, $P=0.008$), in Laelatu D site across all sample plots (n.s.), in Laelatu D site plots 4–9 ($R^2=0.864$, $P=0.023$). Dominant in plots 1–3 is *Filipendula ulmaria* (L.) Maxim., in plots 4–6 *Elymus repens* (L.) Gould, in plots 7–9 *Brachypodium pinnatum* (L.) P.Beauv., in plot 10 *Helictotrichon pratense* (L.) Pilg.. In Aru site $R^2=0.561$, $P=0.008$. (b) leaf nitrogen content per unit leaf area (N_A) in Laelatu D site ($R^2=0.767$, $P=0.003$).

(Fig. 4a). aNUE had no clear trend in D community across all plots. This can be explained by the shift in species composition, more exactly by replacement of the dominant species. *F. ulmaria* dominated in plots Nos. 1–3, where its aNUE was low because of higher foliar nitrogen concentration and despite tall stems. *E. repens* and *B. pinnatum* dominated in the range of plots from 4 to 9. Accordingly, aNUE increased in larger part of the gradient, if plots were regarded separately (Fig. 4a).

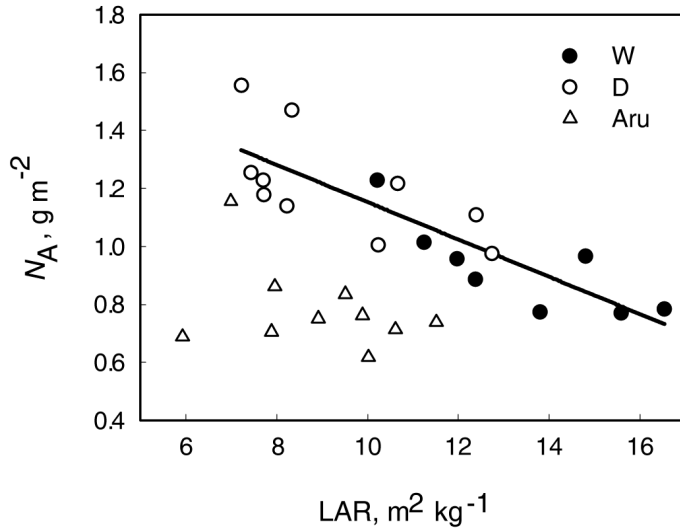


Figure 5. Relationship between community-level leaf area ratio (LAR) and leaf nitrogen content per unit leaf area (N_A) across W and D sites at Laelatu ($R^2=0.698$, $P<0.001$); n.s. in Aru site.

N_A did not show any relationship with site productivity in the monodominant community W (Fig. 4b), while it increased in D site with the rise of above-ground biomass. N_A values were lower in W stand compared to those of D (Table 2 in IV).

3.6. Light-use indices and partitioning of light

In Aru site, canopy-level light absorption per unit of aboveground mass (Φ_M) decreased remarkably with rising stand biomass (Fig. 4 in III). This effect was related at least partially to the increasing cost of supporting tissue, as the LAR of the community diminished. Although light absorption per unit of leaf nitrogen (Φ_N) in Aru decreased with increasing stand biomass in the less productive section of the gradient, the overall relationship revealed no clear trend (Fig. 4 in III). The behaviour of Φ_N at the stand level resulted mainly from the replacement of species with varying species-specific values of Φ_N .

In D site, Φ_M had an optimum and started to decrease beyond it showing that light-use efficiency (LUE) increased at higher productivity (Fig. 4a in IV). The corresponding relationship was not observed in W community. The curve of community Φ_N had an optimum and diminished beyond the optimum with increasing aboveground herbal biomass in D site (Fig. 4b in IV). With respect to the herbal stand of W site, the decline of Φ_N with rise of herb layer biomass was not significant.

3.7. Trade-off between leaf area ratio (LAR) and nitrogen content per leaf area (N_A)

We established a trade-off between community-level N_A and LAR (Fig. 5) in meadow communities at Laelatu. Values of N_A and Φ_N were larger in the dry (D), multi-dominant and low-LAR community; we observed a combination of large LAR and low N_A in the wet site (W), and low LAR and large N_A in the dry site (D).

3.8. Dominants versus subordinates

The species showed contrasting morphological responses to changes in soil fertility. The LAR of all grass species decreased with increasing productivity, although the only significant trend was for *P. pratense*. By contrast, LAR increased in two forb species, *A. millefolium* and *T. officinale* (Fig. 8 in III). Both species, which increased their LAR in response to intensified competition, showed the most plastic response in leaf Chl/N ratio to changes in incident light (Fig. 9 in III). Furthermore, both species had relatively high leaf nitrogen levels and the highest Chl/N ratios in the lower canopy layer, indicating their success in forming robust photosynthetic apparatus under low light conditions and their probable small investments of nitrogen to non-photosynthetic tissues.

Some species (*A. millefolium*, *T. officinale* and *F. pratensis*) exhibited no change in light capture per unit of foliar nitrogen with increasing soil fertility, whereas Φ_N decreased for other species (*C. arvense*, *D. glomerata*) (Fig. 5 in III). Therefore, the increase in stand-level Φ_N in the more productive part of the gradient was caused mainly by the increased domination of *D. glomerata* and *P. pratense* with their relatively high average values of Φ_N . The same explanation is valid for stand-level variation in aNUE, because aNUE was almost invariant to soil fertility with one exception: aNUE in *A. millefolium* decreased with site fertility (Fig. 6 in III).

Similarly, light capture per unit of aboveground dry mass declined along the gradient for two species. However, there was a tendency for the other species to decline as well (Fig. 7 III). However, because the average Φ_M of two grasses, *P. pratense* and *F. pratensis*, was smaller than for the other species, a change in relative abundance with increased productivity amplified the decreasing trend of Φ_M at the stand level (Fig. 4 in III).

4. DISCUSSION

4.1. Two-resource model (I)

The two-resource model can be applied to describe the vertical structure of a multilayer plant community consisting of tree, herb and moss layers (I). One resource can be light and the other nitrogen, because this is the most essential mineral element for plant growth. The biomass of the layers was determined by the relative irradiance reaching the layer and by the amount of nitrogen in the N cycle. We assumed that nitrogen content in foliage reflects the total available nitrogen pool in the soil. We found that a dense tree canopy existed only in combination with high total nitrogen. This finding is in agreement with the idea that trees appear in succession only when a sufficient amount of nitrogen has been trapped in the ecosystem nitrogen cycle (Tilman 1990).

Total foliage mass of the canopy did not increase proportionally with rising amounts of total foliar nitrogen, which means that nitrogen concentrations in thick and productive canopies are higher (Van Keulen et al. 1989). This observation implies that nitrogen-use efficiency declines with increasing productivity in the community. In study I, the foliage dry mass : nitrogen ratio was utilised as an estimate of NUE. Lower vegetation layers demonstrated higher nitrogen-use efficiency or/and better ability to acquire soil nitrogen. The growth of the herbaceous layer in communities along the productivity gradient was co-limited by light and nitrogen; more precisely, it was a compromise between availability of light and nitrogen resources.

To broaden our understanding of the existence of a multilayer structure in plant communities, we analysed our data to answer two questions: (1) what limits the thickness of one layer in a multilayer community, and (2) which traits enable foliage to exist and grow in the shade of the upper layers?

The answer to the first question probably lies in the non-linearity of the relationship between the amount of nitrogen versus intercepted light (Fig. 3 in I). Although photosynthetic production is considered almost proportional to intercepted light (Russell et al. 1989), the discrepancies between actual and theoretical canopy photosynthetic profiles are still poorly understood (Anten 2005). Limits will arise with enlarging amounts of foliage, as the benefit from increased production does not cover the costs of nitrogen needed to construct this foliage as light interception saturates at high leaf area. Light and nitrogen profiles described by Hirose et al. (1988) within two *Lysimachia vulgaris* L. canopies with different densities (Fig. 6 in I) are consistent with our results (Fig. 3 in I). This comparison shows that the relationship between nitrogen versus intercepted light, based on data from different communities, is similar in shape to the relationship within a deep canopy.

Herbaceous plants are able to allocate more nitrogen per unit of intercepted light into their leaves than trees. This probably allows them to build up more powerful light capturing apparatus compared to trees. By contrast, mosses tend

to have low nitrogen concentrations in photosynthesising tissues, but higher NUE than in other vegetation layers, as far as can be concluded from our data (Fig. 5 in I). In addition, as mosses are evergreen plants, their photosynthetic apparatus functions for several years. Eckstein (1999) found that nutrient strategy of moss *Hylocomium splendens*, which dominates in boreal and subarctic forests, is similar to evergreen vascular plants.

Our results also showed that the relative mass of the moss layer was considerable only in low-productive communities with thin overstory canopies and with low amounts of total foliar nitrogen (Fig. 2 in I). Regression analysis showed that growth of mosses was primarily limited by light, so that even high nitrogen availability did not compensate light limitation under deep canopy layers.

4.2. What may give an advantage to graminoids as compared to forbs with increasing site productivity? (II)

Variability of tree layer coverage creates spatial heterogeneity in light conditions within a plant canopy – a primary factor forming the productivity gradient for the herb layer in a multilayer plant community. Variable nutrient availability is the second principal factor, assuming that plant nitrogen content and soil fertility are positively related. Graminoids dominated in high-productive and well-lit habitats both in terms of foliar mass and species number. Three hypotheses were tested to explain better competitive ability of graminoids: (1) they are able to grow higher foliage; (2) they are able to distribute foliar nitrogen vertically in a more efficient way; (3) they are characterized by higher nitrogen-use efficiency.

Vertical distribution of foliage or leaf nitrogen did not differ significantly between the growth-forms along the productivity gradient, and hypotheses (1) and (2) could not be proved. Dominance of graminoids in herbaceous canopy in the high-productive part of the gradient was not caused by the ability to grow higher foliage. Height distribution of forb foliage did not differ between the upper and lower layers along the productivity gradient. This does not mean that dominant species do not have higher foliage, but rather means that forb growth-form is replaced by graminoid growth-form simultaneously in both canopy layers. Hirose and Werger (1995) showed that foliage of dominant species formed the upper layer in the canopy and intercepted most of the incident light, thus suppressing the other species. However, our results show that this explanation does not hold when comparing different growth-forms. However, in studies III and IV we used the same approach that was developed by Hirose and Werger (1995), and revealed that high NUE is a very important characteristic of dominant species, but the morphological plasticity, as regards LAR and its components (SLA and LMF) in particular, is important as well. Vertical distribution of foliar nitrogen follows a com-

mon pattern, where relatively more nitrogen is invested into upper well-illuminated leaves. Plants tend to distribute nitrogen among their leaves in a manner that maximizes whole-plant photosynthesis (Hirose and Werger 1987; Werger and Hirose 1991). In case of the optimal nitrogen distribution, nitrogen concentration in leaves follows the light gradient within a plant canopy (Hirose et al. 1988). In our study, the difference between the growth-forms was not statistically significant, therefore a differential strategy in vertical distribution of foliar nitrogen cannot be responsible for dominance of graminoids in high-productivity sites.

Hypothesis (3) holds partly as the nitrogen concentration in graminoid foliage was on average 20% lower than in forbs. The reciprocal of nitrogen concentration in plant tissue can be used to assess differences in NUE in conditions of equal nitrogen retention time in plants. Nitrogen retention time did not differ between graminoids and forbs in our case, because almost all species identified were perennial in both growth-form groups. McJannet et al. (1995) found that plants with larger above-ground biomass had lower tissue nitrogen levels than smaller plants in the same community and explained it by the high growth rate of bigger plants. Probably low nitrogen content of leaf tissues is associated with high NUE.

Although the influence of growth-form $\times$ productivity interaction on leaf nitrogen concentration was not significant, there was a tendency for the differences in leaf mass to nitrogen ratio (Fig. 7 in II) and aNUE (Fig. 2) between the two growth-forms to increase with increasing incident light. Therefore, we hypothesize that graminoid species dominate in high-productive and well-illuminated plots due to their higher nitrogen-use efficiency compared to forb species.

The present studies carried out at the growth-form level resulted in rather rough findings, because dominants and subordinates may belong to both growth-forms. Therefore, more detailed, species-level studies on aNUE are needed in the future.

4.3. Aboveground biomass allocation patterns and asymmetry of competition

Leaf area ratio (LAR) decreased along two grassland productivity gradients, however, it increased unexpectedly in one site with a rise in community productivity. In high-LAR community, adjustment of leaf morphology via an increase in specific leaf area (SLA) is responsible for LAR increase with rising productivity. In low-LAR stands, two patterns were observed: the LAR dynamics is driven primarily by adjustment of biomass allocation (LMF) or both SLA and LMF are responsible for diminishing LAR with rising productivity. Consequently, a decrease in LAR is not a universal response to increasing aboveground biomass in herbaceous communities.

The directionality of light enables dominant species to monopolize this resource more than soil nutrients and consequently, competitive asymmetry usually increases in high-nutrient soil (Grime 1979; Schippers et al. 1999).

Competitive asymmetry also depends on growth form and usually asymmetry declines under nutrient-poor conditions (Schippers and Kropff 2001). On the basis of two studies (III and IV), we conclude that light competition is more asymmetric in monodominated or mono-species community (with higher LAI and LAR) compared to multispecies communities. More asymmetric light competition is probably caused by similar shoot architecture and leaf arrangement in large and small individuals of the same dominant species. These results are consistent with those by Anten and Hirose (1998): analysis of data from mono-specific *Xanthium canadense* stands revealed that light competition is strongly asymmetrical, because tall individuals absorbed more light per unit of above-ground mass than small individuals.

Anten and Hirose (1999) showed that competition in a multispecies stand was not asymmetric because species have different strategies for biomass partitioning. With increasing intensity of light competition, many plants invest more in height growth, which leads to reduced LAR (Hirose and Werger 1995; Lemaire and Millard 1999). If competition for light is asymmetric (Schippers et al. 1999; Anten and Hirose 2001; Freckleton and Watkinson 2001), relative gains of light absorption with increasing relative mass of a species in the community should be greater in plots with high biomass. If we look at multispecies grasslands in more detail, our data (III) show that relative benefits from enlarged biomass to capture a higher proportion of incident light clearly rise with increasing site productivity (Fig. 2 in III). Consequently, it is clear evidence of increased asymmetry in interspecific competition (Freckleton and Watkinson 2001). Our data suggest that competition for light between species tends to be size-symmetric in stands with LAI < 2.5 and becomes asymmetric above that limit (Fig. 2 in III).

4.4. Nitrogen-use efficiency (NUE)

Berendse and Aerts (1987) found that NUE consists of two components: 1) instantaneous nitrogen productivity and 2) mean residence time of N in the plant. Our studied herbaceous stands belong to steady-state system according to Hirose (2011), i.e. they are perennial communities (not annual). Besides, no woody plants were found in the study areas. Thus, we assumed that mean residence time of N is similar for all plant species. The material was collected at the peak time of vegetation production, consequently we assumed that aNUE should reflect nitrogen productivity.

Study III suggests that species-specific aNUE does depend neither on site productivity nor competitive pressure, even when the biomass allocation pattern (measured as LAR) changes. Our unexpected finding that NUE did not decrease with increasing nitrogen availability either at the species or community level (III) may also be attributed to intensifying competition. If selection favours high nutrient productivity (production per unit nutrient), then the actual trend in NUE

along a productivity gradient should depend on the relative importance and strength of competition. Interactions between species are complex and pair-wise experiments have shown that competitive ability of a species may not change linearly with nutrient availability (Li and Watkinson 2000). A detailed analysis of the components of NUE in a study with 14 plant species growing in two contrasting habitat types showed that nutrient-use efficiency was unaffected by habitat (Eckstein and Karlsson 1997). Van Kuijk and Anten (2009) revealed that whole-canopy NUE was not similar among species belonging to the same functional group.

Study IV revealed that aNUE decreased with increasing productivity in the high-LAR, wet monodominated community. This decrease is attributable mainly to the grass *M. caerulea*, which had relatively low aNUE. In the low-LAR, co-dominated stand, there was no relationship across all sample plots, although aNUE increased across 6 plots dominated by graminoid species. This increase was determined by replacement of dominant species. Grass *E. repens* contributed the most to the community-level rise, exhibiting the highest aNUE. In conclusion, it is difficult to predict the behaviour of NUE.

4.5. Light-use indices and partitioning of light

Hirose and Werger (1995) proposed plant biomass-based calculation of light interception, which has led to an understanding of resource capture partitioning among individuals or species in a stand. We emphasize that in conditions of a productivity gradient and changing LAI, light absorption per unit of above-ground mass (Φ_M) is not predicted solely by morphological traits and spatial arrangement of leaves, but is strongly influenced by light-use efficiency of the plant. It is obvious that when light energy is efficiently converted into biomass, Φ_M may decline even when the available light resource does not change. This fact should be taken into account when interpreting light partitioning data. We found Φ_M to decrease with productivity, as reported by Anten and Hirose (1998, 1999). Therefore, low Φ_M should not be interpreted as a plant's inability to increase light harvesting efficiency, but rather as evidence for increased LUE. Such an increase in LUE is typical when LAI of the community increases (Sinclair and Shiraiwa 1993; Kull and Tulva 2002; Gordillo et al. 2003). The reason underlying such a change in LUE results from the fundamental structure of the photosynthetic apparatus, accordingly increased amounts of photosynthesizing tissue per unit of intercepted light, which ultimately leads to an increase in LUE (Kull 2002).

The results of Paper IV show that light acquisition efficiency (Φ_M) had an optimum at a certain site productivity and beyond that Φ_M decreased in the low-LAR D site (Fig. 4a in IV), showing that LUE increased with rising productivity. However, we did not reveal a corresponding relationship in the high-LAR W community. We hypothesize that a relationship with an optimum exists

between Φ_M and site productivity independent of herbal community type. A decline in Φ_M is an indicator of increased competition for light; because an increase in soil nitrogen availability usually leads to larger LAI and a decline in available light per leaf area or biomass.

Hirose and Werger (1994) proposed to use Φ_N as a measure of NUE. Although, Φ_N in study III showed a high level of conformity with other NUE estimates, one should not use Φ_N as an estimate of NUE ($\Phi_N = \text{NUE}/\text{LUE}$). Consequently, Φ_N can be used as a surrogate measure for NUE only in circumstances when LUE is constant. This assumption is certainly not true for plant stands along a productivity gradient in which LAI changes. We revealed a positive relationship between aNUE and Φ_N in study III, although it varied as LUE changed. However, within species, patterns in Φ_N along productivity gradients (Fig. 5 in III) differed substantially from that of aNUE (Fig. 6 in III). This uncoupling is caused by the systematic trend of LUE along the gradient. The curve of Φ_N in low-LAR D community had an optimum and started to diminish beyond that with enlarging aboveground herbal biomass. On the other hand, the relationship was not statistically significant in the monodominant high-LAR meadow community.

4.6. Trade-off in light- and nitrogen-use

Plant growth in the herbaceous layer in communities situated along a productivity gradient is determined by the relative irradiance above the layer and by nitrogen in the N cycle, as revealed from the two-resource model (I). More precisely, it is a compromise between responses to light versus nitrogen availability.

Hirose and Bazzaz (1998) demonstrated a negative relationship between stand-level nitrogen- and light-use efficiencies and concluded that a plant canopy cannot enlarge its NUE and LUE simultaneously. In study IV a trade-off between foliar nitrogen content (N_A) and LAR was established: the monodominant community was characterized by large LAR and low N_A , while the co-dominated community opposed with low LAR and high N_A . We suppose that this is evidence of a compromise between allocating resources to form larger foliage for greater light acquisition versus utilizing nitrogen resources more efficiently.

4.7. Dominants versus subordinates

The difference in the ability of plant species to acquire and use different resources might be a possible explanation of coexistence (Schulze and Chapin 1987). Every species exhibits unique response patterns to the changes in environment conditions and competition, and combination of traits that assure survival.

Although subordinates are characterized by smaller biomass in communities, they have certain effects on the regenerating of different dominants (Grime 1998). Subsequently, functional diversity between dominant species and probably among subordinates may contribute to an immediate impact on the properties of communities (Grime 1998). For a better understanding of the functioning of herbaceous communities and, more precisely, of the role of subordinates, it is essential to examine the mechanisms that assure survival of subordinates. Why do some species become dominant when productivity increases, whereas others become subordinates? Our results show that the features most likely leading to domination in high-productive sites are intrinsically low LAR and high stature, which allow plant species to overtop others with the cost of a reduction in LAR. Besides, these species have relatively high NUE. One striking difference between dominant and subordinate species observed in this study is their plasticity in LAR. In contrast to dominant species, the subordinates responded to strong competition with LAR enlargement. There are apparently two contrasting adaptive strategies to cope with increased competition: (1) to overtop others with cost of decreasing LAR; or (2) to increase light harvesting ability primarily by increasing LAR.

In addition to the changes in the biomass allocation patterns and exposure of foliage to incident irradiance, changes in foliage light harvesting can occur through modification of leaf pigment contents. Because of the high nitrogen cost of chlorophyll and chlorophyll-binding proteins, within-canopy modifications in light-interception efficiency depend on variations in nitrogen investments in light harvesting (Niinemets 2007). The fact that the subordinates are better adapted to low-light conditions in shade of dominants is also demonstrated by their higher plasticity of adjusting photosynthetic apparatus, as evidenced by changes in Chl/N ratio. Stoichiometry of leaf photosynthetic apparatus changes in a way that at low irradiance there is relatively more chlorophyll-containing, but nitrogen-poor light harvesting apparatus at low irradiance, and less nitrogen-rich biochemical apparatus for electron transport and carbon fixation than at high irradiance (Evans 1989; Eichelmann et al. 2005; Hikosaka 2005). In addition, species differ largely in their ability to adjust their photosynthetic apparatus for particular PPFD conditions (Turnbull et al. 1993; Murchie and Horton 1997; Kursar and Coley 1999). Our study shows that subordinate species deprived of a strategy to grow tall in response to intensified competition for light are more plastic in adjustment of their photosynthetic apparatus to shade. Therefore, the ratio of leaf chlorophyll to nitrogen content is more responsive in subordinate species compared to dominant species.

5. CONCLUSIONS

- 1) A two-resource model is a suitable tool to describe the vertical structure of a multilayer plant community. The biomass of the vegetation layer is determined by the relative irradiance above the layer and the amount of nitrogen in the cycle. The overstory receives light resource in large quantities compared to lower vegetation layers, while the lower layers have higher nitrogen-use efficiency and/or a better capability to acquire nitrogen. The two-resource model well explains the co-limitation of growth of the herbaceous layer by light and nitrogen availability. The growth of the moss layer is limited primarily by light availability.
- 2) Graminoid species dominate in high-productive and well-illuminated sites in grassland communities probably due to their higher nitrogen-use efficiency when compared to forb species.
- 3) A decrease in leaf area ratio (LAR) is not a universal response to increasing aboveground biomass in herbaceous communities. While LAR decreased in two grassland communities with increasing site productivity, it unexpectedly increased in one site with a rise of productivity. In a high-LAR community, adjustment of leaf morphology via change in specific leaf area (SLA) is responsible for an increase in LAR with rising productivity. In low-LAR stands, rather a modulation of both leaf mass fraction (LMF) and SLA is responsible for diminishing LAR with rising productivity.
- 4) Competition for light is more asymmetric in a monodominated or monospecies herbaceous community (with higher LAI and LAR) compared to two multispecies communities. More asymmetric light competition is probably caused by similar shoot architecture and leaf arrangement in large and small individuals of the same dominant species.
- 5) In a low-LAR community, light acquisition efficiency (light absorption per unit of aboveground biomass, Φ_M) declined at the community level and also in most species. Whereas on the basis of two other grasslands (one low-LAR and one high-LAR), the hypothesis may be established that an optimum of Φ_M exists along a productivity gradient independent of herbaceous community type. Accordingly, a question concerning the Φ_M versus aboveground dry mass relationship remains: does a certain optimum exist in other (herbaceous) community types as well?
- 6) There is no universal pattern of aNUE for different plant communities with increasing site productivity. Variation in aNUE with respect to environmental conditions remains uncertain. Therefore, it is essential to examine this issue further in different dominant and subordinate species in various communities.

- 7) A trade-off between leaf nitrogen content per unit leaf area (N_A) and LAR was established in two herbaceous communities: the wet monodominant community was characterized by large LAR and low N_A , while the dry co-dominated community opposed with low LAR and high N_A . There exist two contrasting types of plastic responses: first type of plants responds to rise in soil fertility and light competition with increasing LAR; in the second type of plants LAR reduces. Plants have to compromise between effective light-use, nitrogen-use and biomass allocation to better accomplish one of these resource uses.
- 8) Different life strategies exist among plant species within particular growth-form, while a set of characteristics depends also on the species position in the community: is it dominant or subordinate? There are clear differences in acclimation patterns between species that become dominant and that remain as subordinates. More precisely, plasticity in aboveground growth patterns and nitrogen allocation differs among species in response to increased soil fertility and competition, thus leading to substantially different strategies for survival. Subordinate species deprived of the ability to grow tall in response to intensified light competition are more plastic in the adjustment of their photosynthetic apparatus to shade conditions, and the ratio of leaf chlorophyll to nitrogen content is more responsive in subordinates than in dominant species.

Tasks for the further studies:

- 1) Patterns of NUE (aNUE) with respect to environmental conditions remained uncertain. Therefore, it is essential to examine this issue in different species inhabiting various communities in more detail.
- 2) A question concerning the Φ_M versus aboveground dry mass relationship: does a certain optimum exist in other community types as well?

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SUMMARY IN ESTONIAN

Valguse ja lämmastiku kasutamine ning biomassi allokatsioon produktsiooni gradientidel mitmerindelistes taimekooslustes

Taimede ellujäämiseks, kasvuks ja edukaks paljunemiseks on vajalik keskkonnaressursside piisav kättesaadavus. Kõige sagedamini limiteerivad taimede kasvu valgus ja mulla lämmastik. Lämmastiku omastamine mullast on taime jaoks väga energiakulukas protsess. Sellest lähtuvalt on oluline, et taim kasutaks nimetatud ressursse võimalikult efektiivselt. Millised on koosluse- ja taimesisesed allokatsioonimustrid (nt biomassi ja lämmastiku puhul), et paremini kohaneda antud kasvukoha tingimustega? Sellele vastamiseks uuriti antud töös muutusi valguse ja lämmastiku kasutamises taimeliikide ning koosluste tasandil piki produktsiooni gradienti looduslikes taimekooslustes. Produktiivsusgradient võimaldab uurida taimi iseloomustavate tunnuste varieerumist ning nende plasilisust keskkonnafaktorite ja konkurentsi intensiivsuse gradatsioonis.

Doktoritööle püstitatud eesmärgid ja saadud põhitulemused (vastavalt artiklite järjestusele dissertatsioonis) olid järgmised.

1. Analüüsida valguse neeldumist ning lämmastiku ja lehemassi jaotumist mitmerindelise taimekoosluse erinevate rinnete vahel (I). Vaatluse all olid erineva avatusega taimekooslused: niidu-, puisniidu- ja heitlehine metsakooslus. Proovialad, mida oli kokku 21, paiknesid Lääne-Eestis Laelatu puisniidul piki produktsiooni gradienti. Prooviruutudel mõõdeti taimkatte rinnetes neelduv valgus, arvutati puurinde lehestiku kuivmass, määrati rohu- ja samblarinde biomassid. Lämmastiku sisaldus määrati puu- ja rohhtaimelehtedes ning sambla elavates osades. Püstitatud eesmärgi lahendamiseks konstrueeriti mudel, mis kirjeldab lehestiku massi vertikaalset jaotumist koosluses sõltuvalt kättesaadava lämmastiku ja valguse hulgast.

Uurimuse tulemusena selgus, et ülemise rindeni jõuab suurema intensiivsusega valgusvoog, võrreldes alumiste rinnetega. Alumisi rindeid iseloomustab efektiivsem lämmastiku kasutamine ja/või parem võime omastada mullast lämmastikku. Kaheressursilise mudeli rakendamisest järeldub, et rohurinde kasvu piki produktsiooni gradienti limiteerivad nii kättesaadav valgus kui ka lämmastik. Samblarinde kasvu limiteerib rindele peale langev valguskiirguse voog.

2. Selgitada, mis annab graminoididele niidukoosluses domineerimiseks eelise, võrreldes rohundite kasvuvormiga (II). Täpsustavalt uuriti, kas graminoidide domineerimine on põhjustatud a) erinevustest lehestiku vertikaalses jaotumises, b) erinevast lämmastiku vertikaalsest jaotumisest lehestikus, c) erinevustest lämmastiku kasutamise efektiivsuses. 21 prooviruutu paiknesid Laelatu puisniidul piki produktsiooni gradienti. Ruutudel mõõdeti rohurindele pealelangev suhteline valguse intensiivsus ning rindes neeldunud valgus.

Rohurinde maapealne osa eemaldati 50×50 cm suurustelt ruutudelt kahe kihina. Kihid eraldati teineteisest kõrguselt, kus oli neeldunud pool kogu rohurindele langevast valguskiirgusest. Rohttaimed sorteeriti kihiti rohunditeks ja graminoidideks ning need fraktsioonid omakorda lehtedeks ja muudeks organiteks. Rohundite ja graminoidide lehtede lämmastiksisaldus määrati mõlemas kihis eraldi.

Tulemuseks saadi, et graminoidid hakkasid domineerima kõrge produktiivsusega ja intensiivse valguskiirgusega kasvukohtadel nii lehtede suhtelise massi kui ka liikide arvu poolest. Lämmastiku kontsentratsioon graminoidide lehtedes oli 20% madalam kui rohundite lehtedes. Püstitati hüpotees, et graminoididel on rohunditega võrreldes kõrgem lämmastiku kasutamise efektiivsus ning tõenäoliselt seetõttu saavad nad domineerida kõrge produktiivsuse ja valgusintensiivsusega kasvukohtadel.

Eelnevad tööd näitasid vertikaalsete kihtide arvu suurendamise vajalikkust niidukooslustes, et uurida suurema täpsusega valguse ja lämmastiku kasutamise näitajate käitumist ning biomassi allokatsiooni muutumist sõltuvalt kasvukoha viljakusest. Seetõttu püstitati III ja IV artiklis järgmised eesmärgid.

3. Rakendada Hirose ja Wergeri (1995) poolt väljatöötatud meetodit valguse jaotumise uurimiseks rohustute produktiivsusgradientidel ning võrrelda valguse kasutamise muutumist keskkonnatingimuste varieerumisel koosluse ja ohtramalt esinevate liikide tasandil.
4. Hinnata lämmastiku kasutamise efektiivsust (NUE) kasvukoha produktiivsusgradiendil koosluse ja liikide tasandil.
5. Selgitada, kas lehepinna suhte (LAR) vähenemine on universaalne reaktsioon maapealse biomassi suurenemisele niidukooslustes, ning täpsustada, milline LAR-i komponentidest – kas lehe eripind (SLA) või lehestiku suhteline mass (LMF) – põhjustab LAR-i muutumist sõltuvalt kasvukoha viljakusest.
6. Võrrelda valguse neelamise võimet ja NUE-d niidukooslustes, millel on erinev biomassi allokatsioonimuster, ning selgitada, millised omadused annavad eelise dominantidele ja mis võimaldavad alusliikidel dominantide varjus ellu jääda.
7. Analüüsida, kas esineb lõivsuhe LAR-i ja pindalaühiku kohta väljendatud lehe lämmastiksisalduse (N_A) vahel.

Vastuste leidmiseks koguti materjal ühest rohumaakooslusest Tartumaal Elva lähedal Arul (III) ning kahest niidukooslusest Läänemaal Laelatul (IV). Arul märgiti 10 prooviruutu (suurusega $0,5 \times 0,5$ m) rohumaale, mis oli kujunenud ligikaudu viie aasta eest söötijäetud põllumaale. Valgusintensiivsust mõõdeti kvantsensoriga rohustu kohalt ja kõrguskihtide piiirilt koosluse seest. Mõõtmiste põhjal arvutati erinevates kihtides neeldunud valguse hulk. Ruudult eraldati kihtide kaupa taimede maapealsed osad, 3–5 kihti vastavalt rohustu kõrgusele. Määrati iga kihi liigiline koosseis ja iga liik sorteeriti kahte fraktsiooni: lehed ja muud organid. Lämmastikuanalüüsid määrati

kihtide kaupa rohkem esinevate liikide lehtedest ja mullaproovidest, millest leiti ka mulla kuivainesisaldus.

Laelatul (IV) paiknesid prooviruudud ($0,5 \times 0,5$ m) kahel transektil piki produktsiooni gradienti: liigniiske mullaga koosluses 8 ja parasniiske mullaga rohumaal 10. Valguse intensiivsust mõõdeti lintpüranomeetriga rohustu kohalt ja kõrguskihtide piirilt koosluse seest. Järgnev metoodikaosa on analoogne III artiklis rakendatuga.

Uuriti järgmiste parameetrite käitumist produktsiooni gradiendil: lehepinna indeks (LAI), lehepinna suhe (LAR), lehe eripind (SLA), lehestiku suhteline mass (LMF), valguse omastamise efektiivsus e valguse neeldumine taimede maapealse massiühiku kohta (Φ_M), valguse neeldumine lehe lämmastikuühiku kohta (Φ_N), maapealne lämmastiku kasutamise efektiivsus (aNUE), lehe lämmastikuisisaldus lehe pindalaühiku kohta (N_A) ja konkurentsi asümmeetría parameeter (B).

III ja IV uurimusest tehti järgmised olulisemad järeldused.

LAR-i vähenemine ei ole universaalne reaktsioon produktiivsuse suurenemisele rohumaakooslustes. Kahel uuritaval gradiendil LAR vähenes, aga vastuootusi ühel gradiendil suurenes koos kasvukoha produktiivsuse tõusuga. Suure LAR-iga koosluses toimus LAR-i tõus SLA suurenemise tulemusel, st lehe morfoloogiliste tunnuste muutumise tagajärjel. Väikese LAR-iga kooslused reageerisid keskkonnatingimuste paranemisele mõlema LAR-i komponendi muutumisega: LMF-i vähenemise ja SLA suurenemisega.

Valguskonkurentsi asümmeetría (parameeter B) on suurem ühe domineeriva liigiga ja suurema lehepinna indeksiga (LAI) koosluses, võrreldes kahe uuritud mitme dominandiga rohustuga. Asümmeetrilisem valguskonkurentis on tõenäoliselt tingitud sama dominantliigi juveniilide ja fertiilsete isendite sarnasest võsude arhitektuurist ja lehtede asetusest.

Valguse omastamise efektiivsus (Φ_M) vähenes ühe madala LAR-iga rohustus nii koosluse tasandil kui ka mõnedel liikidel. Kahe ülejäänud koosluse (üks madala, teine suure LAR-iga) põhjal saab püstitada hüpoteesi, et valguse omastamise efektiivsuse muutumist produktsiooni gradiendil iseloomustab optimumiga kõver. Järgnevates uurimustes oleks vajalik välja selgitada, kas analoogiline optimumiga kõver kehtib ka teiste taimekoosluste puhul.

Valguse neeldumine lehe lämmastikuühiku kohta (Φ_N) väljendab lämmastiku ja valguse kasutamise efektiivsuste suhet (NUE/LUE). Ühes madala LAR-iga koosluses ei esinenud seost Φ_N ja produktiivsuse vahel, kuna mõlemad efektiivsused (nii LUE kui ka NUE) suurenesid. Antud koosluse mõnedel liikidel esines Φ_N vähenemistendents, sest nende NUE produktsiooni gradiendil ei muutunud. Teise, madala LAR-iga rohustu puhul täheldati optimumiga seost; suure LAR-iga koosluses seos puudus.

Koosluse tasandil kasvas aNUE rohustu produktsiooni suurenedes ühel uuritud transektidest (madala LAR-iga koosluses). Samas tuleb rõhutada, et aNUE suurenemise põhjustas liikide vaheldumine produktsiooni gradiendil.

Teise, madala LAR-iga koosluse puhul ei leitud seost aNUE ja maapealse biomassi vahel terve gradiendi ulatuses, kuigi kuuel prooviruudul kümnest, kus domineerisid kõrrelised, täheldati rohustu biomassi suurenemisel aNUE tõusu. Madala LAR-iga monodominantses hariliku sinihelmika (*Molinia caerulea* (L.) Moench) koosluses tõusis aNUE produktsiooni suurenemisel. Veel on ebaselge aNUE reaktsioon keskkonnatingimuste muutumisele, eriti liikide tasandil, ning see vajab edasist uurimist erinevates kooslustes, arvestades sealjuures liigi staatust koosluses (dominant või alusliik).

Kahes uuritud koosluses (üks madala, teine kõrge LAR-iga rohustu) leiti lõivsuhe LAR-i ja N_A vahel. Monodominantset kooslust liigniiskel mullal iseloomustasid suur LAR ja madal N_A , aga mitme dominandiga kuival mullal esinevas niidukoosluses oli väike LAR ja kõrge N_A . Seega esineb teatav kompromiss valgusressursi ja lämmastikuressursi paremaks kasutamiseks tehtavate kulutuste vahel.

Liikide omavahelisel võrdlemisel selgus, et dominandid ja alusliigid reageerivad kasvutingimuste muutustele täiesti erinevalt. Täpsemalt, liikide maa-pealse biomassi ja lämmastikuisalduse jaotumise plastilisuse varieeruvus tekitab erinevad valguse ja lämmastiku kasutusmusterid ning sellest tulenevalt kujunevad erinevad ellujäämisstrateegiad.

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Ema head soovid on mind ikka saatma jäänud...

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Valguse, lämmastiku ja biomassi jaotumine rohurindes

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