

MARI LEPIK

Plasticity to light in herbaceous
plants and its importance
for community structure and diversity



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248

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plants and its importance
for community structure and diversity



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LIST OF ORIGINAL PUBLICATIONS

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

- I. **Semchenko M, Lepik M, Götzenberger L, Zobel K.** 2012. Positive effect of shade on plant growth: amelioration of stress or active regulation of growth rate? *Journal of Ecology* **100**: 459–466.
- II. **Lepik M, Liira J, Zobel K.** 2005. High shoot plasticity favours plant coexistence in herbaceous vegetation. *Oecologia* **145**: 465–474.
- III. **Lepik M, Zobel K.** 2013. Positive relationship between small-scale species richness and shoot morphological plasticity – is it mediated by ramet density or is there a direct link? Manuscript.
- IV. **Lepik M, Liira J, Zobel K.** 2004. The space-use strategy of plants with different growth forms, in a field experiment with manipulated nutrients and light. *Folia Geobotanica* **39**: 113–127.

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The author's contribution to the papers:

	I	II	III	IV
Designing the experiments	*	*	*	*
Data collection	*	*	*	*
Analyzing the results	*	*	*	*
Manuscript preparation		*	*	*

I. INTRODUCTION

I.1. Plasticity to light conditions

Solar radiation is an essential resource for green plants, which inhabit most of the terrestrial environment in communities with highly variable diversity, density, productivity and complexity. Amidst this heterogeneity, individual plants are capable of gathering comprehensive information about the ecological characteristics of surrounding vegetation, including the light climate. In addition to certain “olfactory senses” – distinguishing chemical information like nutrient levels, root exudates or volatile compounds – plants have a rather well developed “visual sense” (Pierik et al. 2012). For plants, light quality and quantity carry important information about the competitive situation above-ground, in the present and in the close future (Ballaré et al. 1988, Aphalo et al. 1999, Franklin 2008, Novoplansky 2009, Pierik et al. 2012). Depending on growth conditions, genetically determined traits and ontogenetic stage there is a wide range of ways that environmental information can be captured by plants and how plants are adapted to react to it (Ballaré et al. 1988, Aerts et al. 1991, Aphalo et al. 1999, Liira and Zobel 2000, Urbas and Zobel 2000, Franklin 2008, Leyser 2009, Novoplansky 2009, Nyanumba and Calhill 2012, Pierik et al. 2012). Plants' acclimatization to habitat conditions is primarily limited by their basic morphology (Díaz et al. 1998), reflecting their fixed phylogenetic adaptations (Cody 1991). These restraints dictate general acclimatization strategies for resource acquisition and partitioning (Aerts et al. 1991, Kull and Aan 1997, Liira and Zobel 2000) and form the basis of species synecological requirements.

Both biotic and abiotic environmental factors modify plant growth through genetically determined and epigenetically regulated reaction norms, resulting in phenotypic plasticity – the capacity of a given genotype to produce different phenotypes under different environmental conditions (Scheiner 1993, Aubin-Horth and Renn 2009). Although plasticity evolves more or less independently of other plant traits, part of the variability in plant characteristics originates directly from allometric relationships between phenotypic traits and plant size or ontogenetic stage (McConnaughay and Coleman 1999, Wright and McConnaughay 2002, Weiner 2004, Janeček et al. 2013). Depending on the study objective, adaptive transformations in phenotype resulting in changes of size-allometry or ontogeny may also be referred to as phenotypic plasticity (Schlichting and Pigliucci 1998, Gianoli and Valladares 2012). Various approaches to this problem have created a situation where studies using different plasticity-estimating methods describe different aspects of acclimatization ability (reviewed by Wright and McConnaughay 2002 and Valladares et al. 2006). As a response to the broad variety of opportunities for acclimatization to changing environment, plants demonstrate a myriad of strategies (which also interact with each-other) to deal with varying and complex conditions in dense multi-species stands.

1.2. Possible nexus between plasticity and community structure

Even in apparently homogenous stands, the number of ramets and species per unit area may differ greatly between micro-sites, and variation between community types is naturally even more extensive (Zobel and Liira 1997). The number of theories and models describing processes underlying community formation is remarkably high (*habitat filtering*, Keddy 1992, Jung et al. 2010; *carousel model*, van der Maarel and Sykes 1993; *trait-environment linkage*, Diaz et al. 1998; *species pool concept*, Pärtel 2002, Cornwell and Grubb 2003; *mid-domain effect*, Colwell et al. 2004; *neutral theory and ecological equivalence*, Hubbell 2006; *trait-based selection*, Sonnier et al. 2010; to mention only few examples; see Ricklefs 2004, Keddy 2005, McGill et al. 2007 or Gravel et al. 2011 for review). The most suitable theory for a particular ecological situation depends on the study scale and on the precise questions asked (McGill et al. 2007, Wennekes et al. 2012). It is evident that the functional traits of species present in the community species pool to a large extent determine the structure and diversity of plant communities (Díaz et al. 1998, de Bello et al. 2012). Among the many functional traits considered in this context, morphological plasticity has received little attention and has rarely been causally linked to environmental filters (Sonnier et al. 2010). This thesis is based on an assumption that the degree of morphological plasticity among co-existing plants could significantly affect the survival of individuals in communities and could thus be an important determinant of plant density as well as species diversity.

It has been proposed that high shoot plasticity may improve the ability of plants to adjust to high ramet density and thus reduce the degree of competition asymmetry in crowded stands (Weiner et al. 1990, Schmitt and Wulff 1993, Sorrensen-Cothorn et al. 1993, Schwinning and Weiner 1998, Chesson 2000, Stoll et al. 2002, Vermeulen et al. 2008). The usual response of plastic plants to a close neighbour is to reduce branching, thus avoiding the shade cast by the neighbour and decreasing the overall competitive effect (Callaway et al. 2003; Herben and Novoplansky 2010, Wennekes et al. 2012). Consequently, high average shoot plasticity could be viewed as an intra-community *stabilizing force*, causing species to limit themselves more than it does others (i.e. through shade avoidance syndrome), and an *equalizing force*, operating to reduce inherent differences in species performance, increase resource-use complementarity and thus promote coexistence (Callaway et al 2003, Wacker et al. 2009, Lankau 2011).

The main purpose of plasticity is to widen the breath of an individual's ecological niche and therefore relieve the effect of environmental filters. Thus, mortality caused by biotic or abiotic filtering or drift should be lower for individuals and species with high acclimatization ability (reviewed by Valladares et al. 2007, Chevin et al. 2010, Reed et al. 2010, Jung et al. 2010, Lankau 2011, Andersen et al 2012). At the stand level this could result in a

higher ramet density and therefore higher local species diversity per unit area as well. One could speculate that in certain cases higher plasticity should also result in an increase of species diversity per ramet (not only per unit area), due to decreased local extinction. High phenotypic variability (either due to plasticity or genetic differences) is expected to enhance niche partitioning, level off differences in competitive ability and provide certain privileges to rare genotypes or species (Levine and HilleRisLambers 2009, Jung et al. 2010, Lankau 2011; but see Vermeulen et al. 2008), thus promoting coexistence and increasing scale-independent diversity in highly plastic communities. However, to the best of my knowledge, the possible effect of mean morphological plasticity in local plant assemblages on community diversity has never been tested.

Species diversity in plant assemblages is known to be a function of ramet density – at high densities neutral or species-specific self-thinning is expected (Oksanen 1996, Stevens and Carson 1999). On the other hand, species richness per unit area is known to positively depend on ramet density (Oksanen 1996, Zobel and Liira 1997). In certain conditions positive interactions are invoked to explain the structure and diversity of communities (Aphalo et al. 1999, Michalet et al. 2006). Facilitation by neighbors is vital for plants inhabiting stressful conditions, where non-competitive exposed habitats are characterized by an increased importance of herbivory relative to competition, high risk of mechanical damage, photoinhibition, drought or thermal stress (Schmitt 1997, Callaway et al. 2003, Ray et al. 2004, Ballaré 2009, Dickson and Foster 2011). Although facilitation is often masked by much stronger negative interactions, it may, in addition to increased productivity, lead to higher diversity, and not only in extreme habitats (Michalet et al. 2006, Gross 2008, Cavieres and Badano 2009, Dickson and Foster 2011, Nyanumba and Cahill 2012). Phenotypic plasticity has been proposed as a factor mediating the shift between the two extreme types of interaction – competition and facilitation (Callaway et al. 2003). The relative role of facilitative interactions in those processes that govern the structure and diversity of temperate grasslands is currently unknown.

It is reasonable to assume that the mechanisms through which plasticity affects plant-plant interactions and thus community structure could often be related to the light resource. In high productivity communities light becomes the limiting resource for plants of lower height (van Hinsberg and van Tienderen 1997, Rajaniemi 2002) leading to strong competition asymmetry (Schwinning and Weiner 1998, Aphalo et al. 1999). Thus, plasticity to light could be an important trait in competitive situations where intense self-thinning processes can drastically alter the spatial structure and species diversity in a plant assemblage (Stevens and Carson 1999). To retain competitive ability above-ground, plants growing in productive communities usually increase allocation of photosynthates into shoots (van Hinsberg and van Tienderen 1997, McConnaughay and Coleman 1999, Ryser and Eek 2000; but see Casper et al 1998). This, along with adaptive changes in plant architecture and physiological parameters, helps to improve light acquisition and avoid competitive exclusion

in dense canopies (Sultan 1995). Plastic reactions to shade have been demonstrated to result in complex changes of plant growth pattern, starting with high investments into apical rather than radial growth, reduced branching, thinner leaves, changed leaf orientation and angle, etc. (*shade avoidance syndrome*; Ballaré et al. 1988, Dong and deKroon 1994, van Hinsberg and van Tienderen 1997, Huber and Wiggerman 1997, Maddonni et al. 2002, Pierik et al. 2012). Rearrangements in architecture and physiology significantly enhance light absorption of acclimatized plants in crowded stands, when compared to non-plastic individuals (Ballaré et al. 1988, Maddonni et al. 2002). The effect of plastic acclimatization to light climate on community structure is expected to be complex and has not yet been studied in detail.

Although there are numerous plant species whose fixed strategy is to out-compete neighbours through resource-preemption, the usual response of a morphologically plastic plant to a neighbor is competition avoidance through physical avoidance, above-ground or below-ground (Schwinnig and Weiner 1998, Maddonni et al. 2002, Callaway et al. 2003, Novoplansky 2009, Herben and Novoplansky 2010). Shoot distance-keeping is often mediated by shade avoidance syndrome, which is known to result in reduced competition between individuals by diminishing competition asymmetry (Schwinnig and Weiner 1998, Aphalo et al. 1999, Vermeulen et al. 2008) and increasing resource-use complementarity through character displacement (*niche partitioning*; Callaway et al. 2003, Wacker et al. 2009, Jung et al. 2010). The decrease of negative interactions between neighbouring ramets has been shown to be especially apparent when plants with different morphology (and also physiology) grow in a mixture (Tilman et al. 1997, Stoll et al. 2002, Isbell et al. 2009, Burns and Strauss 2012). The decrease of competitive pressure with character displacement has been shown to occur within species (Stoll et al. 2002, Kotowska et al. 2010) as well as between species (Tilman et al. 1997, Fridley 2003, Vojtech et al. 2007, Isbell et al. 2009). It has even been suggested that phenotypic variability caused by plasticity could in some cases be more important than interspecific niche differences for the overall reduction of competitive pressure in communities (Stoll et al. 2002, Jung et al. 2010). However, this has not been properly tested in natural multi-species stands.

When considering the possible effect of species plasticity on community processes it is important to acknowledge that restrictions on the allocation pattern and spatial distribution of biomass are imposed by the basic morphological features of species. Basic morphology reflects plants' phylogenetic adaptations for resource acquisition and partitioning (Cody 1991), but also determines the limits and nature of ontogenetic adaptations (plasticity) to differences in resource availability. When grouping herbaceous species according to essential morphological features, i.e., growth form, one may see that this also indicates a certain general strategy in resource acquisition, and brings along a specific pattern of plastic responses to changing resource availability levels (Aerts et al. 1991, Hirose and Werger 1995, Mitchley and

Willems 1995, Kull and Aan 1997, Liira and Zobel 2000). Thus, it is logical to expect that space-use strategy with changing resource levels is probably not only species-specific but also growth-form-specific. This thesis attempts to study how space-use strategy, a specific plastic trait, is related to the basic growth-form characteristics of grassland plants.

Debate concerning the consequences of plastic acclimatization on the evolution and interactions of plant species, and ecosystem functioning etc., has been ongoing for more than 100 years (Metcalf 1906, Fuller 1920, Bradshaw 1965, Callaway et al. 2003, Fordyce 2006, Jung et al. 2010, Laughlin and Laughlin 2013 etc.). Nonetheless, there are several aspects that are relatively understudied or that exist only as theories (Callaway et al. 2003, Keddy 2005, Laughlin and Laughlin 2013). The lack of standard methodology for estimating plasticity comparably across different species and traits has inhibited research into the role of phenotypic plasticity in community processes. Thus, largely for methodological reasons, there are practically no empirical studies on the effect of plasticity on community structure in natural multi-species stands. Using a novel methodology, parallel to a more common approach to plasticity estimation, this thesis attempts to shed further light on the issues discussed above.

I.3. Main aims of the thesis

The main purpose of this thesis was to understand the role of shoot morphological plasticity as a plant functional trait in community processes. This thesis incorporates autecological and synecological studies, aiming to demonstrate that the degree of morphological plasticity to light in co-existing species, as well as species' basic growth-forms are important predictors of grassland community structure and diversity. This thesis incorporates autecological and synecological studies, aiming to demonstrate that the degree of morphological plasticity to light in co-existing species is an important predictor of grassland community structure and diversity. More specifically, we wanted to investigate the following points:

1. We wanted to achieve precise and comparable shoot plasticity estimates for a representative number of herbaceous plant species (**II**). We also wanted to find out how species plasticity to light availability is related to other basic traits (growth rate, synecological demands, basic morphological characteristics), using both size-dependent (**I**) and size-independent plasticity estimates (**II**).
2. We wanted to learn how size-independent morphological plasticity to light affects community structure and diversity in temperate herbaceous stands (**II, III**).
3. We wanted to find out the effect of moderate shift in resource availability in above- and below-ground on an herbaceous assemblage structure (biomass density vertical distribution and growth-form specific biomass density adjustments; **IV**).

2. MATERIALS AND METHODS

2.1. Growth and plasticity of 46 herbaceous species along a gradient of light availability

Species morphological plasticity and growth along a light gradient was assessed in a garden experiment. In ecological studies it is recommended to use plasticity across species not genotypes (Gianoli and Valladares 2012). Seeds of 46 randomly chosen perennial herbaceous species were collected from a range of temperate grassland communities in Estonia. Twenty similar-sized seedlings of each species were planted, one seedling per pot, into 1.2-L pots filled with fine sand. Plants were distributed equally among four spectral neutral shading treatments: 10%, 25%, 50% and 100% daylight. Three structures with tops and sides covered by shading cloths were constructed to provide shading treatments. Plants were left uncovered in the 100% daylight treatment. After 10 weeks of growth plants were harvested. Plant leaf area was measured and leaf number counted, plants were dried at 75° C for 24 h and weighed.

We used two types of index to describe species phenotypic responses to light availability – the relative difference in trait values in response to light treatments (size-dependent plasticity; **I**) and the slope of the trait reaction norm (for this the allometric effect of biomass was removed; size-independent plasticity; **II** and **III**).

To compare plant performance in full light and in moderate shading we made comparisons between the 100% daylight treatment (*meanfull*) and the 50% shading treatment (*mean50*). The relative difference in trait means was calculated as $(mean50 - meanfull)/(mean50 + meanfull)$ for plant biomass, leaf area ratio (LAR) and specific leaf area (SLA). These indices range from -1 to +1, with negative values indicating a decrease and positive values an increase in trait means in 50% daylight, compared with full daylight (**I**). Changes in LAR in response to light treatments were used as estimates of species morphological plasticity, as suggested for interspecific comparisons by Valladares et al. (2006).

The second estimate of size-independent morphological plasticity (**II**) in response to illumination was defined as the absolute value of the slope of the reaction norm between trait value and light availability (Scheiner 1993, Pigliucci and Schmitt 1999). Such a plasticity estimate is comparable across different traits and species, provided that the trait value is log-transformed and the allometric effect of biomass is considered and removed. We estimated plasticity for all 46 species in two leaf traits – mean leaf area (Π_{LA} ; **II**, **III**) and number of leaves (Π_{LN} ; **II**) using generalized linear models (GLZ; Statistica 6.0, StaSoft Inc., Tulsa USA) with logarithmic trait values as dependent variables and two continuous independent components: environmental factor (experimentally manipulated light) and plant biomass with necessary modifications to account for size-dependent variation in the trait value (see **II** for a detailed description of the methodology). In **II** we calculated overall shoot plasticity for

each species as the Euclidian distance between the two estimates: $\Pi = (\Pi_{LA}^2 + \Pi_{LN}^2)^{-0.5}$ (the recommended statistic in the case of presumably closely correlated variables; Sokal and Rohlf 1995) and used it as the dependent variable.

To test the first aim of this thesis we analyzed whether the estimated size-independent shoot plasticity of species (Π in **II**) and relative difference in trait values in response to light treatments (size-related plasticity; **I**) are associated to other plant characteristics that we presumed to be important: basic morphology, synecological requirements and plant height. We compared the plasticity and space use strategy in changing environmental conditions of species with different growth forms (according to basic shoot characteristics – leaf width narrow/wide and presence/absence of leafy stem; Liira and Zobel 2000; **II**, **IV**). The synecological requirements of species (for light and nutrient availability) were described using Ellenberg's indicator values (Ellenberg et al. 1991; if unavailable for continental Europe, indicator values for the British flora were used, Hill et al. 1999; **I** and **II**). Ellenberg's indicator values for nitrogen and water were also used to describe species ecological optima and their tolerance of abiotic stress (**I**). We also tested for the possible effect of plant species mean height in the full-light treatment on shoot plasticity (Π ; **II**).

2.2. Intra-community study in Laelatu calcareous wooded meadow

Interrelations between species plasticity and community structure were examined in a mesic calcareous wooded grassland in western Estonia (Laelatu wooded meadow, 58°35' N, 23°34' E) in two permanent-plot studies. The meadow has a scattered tree layer with *Quercus robur*, *Fraxinus excelsior*, *Corylus avellana*, *Betula* spp. and *Populus tremula* as the most abundant species, with average total coverage of ca. 30%. The meadow has been annually mown for hay in early July for more than 200 years. The perennial-dominated herbaceous community is very rich in species at a small-scale (up to 68 species per 1 m²; Kull and Zobel 1991).

Permanent plot study 1 (Papers **II and **IV**)**

The first field experiment started in 1994. Vegetation in 24 40×40 cm permanent plots was treated with annual fertilization and additional illumination with mirrors, using a randomized factorial design. Half of the plots were fertilized with a water solution of N (10 g m⁻² y⁻¹), P (4.2 g m⁻² y⁻¹), K (4.2 g m⁻² y⁻¹) and microelements in May and September, while half of the plots received additional illumination. In conditions of direct sunlight, the vertically placed 123×212 cm glass mirrors increased the intensity of PAR by 60% compared to non-illuminated conditions (measured with linear light meter Licor LI-250). Availability of direct PAR in sample plots (T_{dir}) was estimated from hemispherical photographs in 1998. To account for the effect of mirrors,

an additional illumination coefficient (C_{ai}), describing the proportion of total radiation provided by mirrors, was estimated for each permanent plot with a mirror from the hemispherical photograph. An index of direct light availability (DLA) was calculated for each permanent plot: $DLA = T_{dir} (1 + C_{ai})$ (IV). Vascular plant species were recorded in all 24 plots in early July for five years (1994–1998; II).

Biomass data were collected from the above-described permanent plots in 1998 (IV). In each 40×40 cm permanent plot, above and below-ground biomass was collected from four 8 cm diameter circular areas (subplots). Since we wanted to disturb the vegetation in permanent plots by destructive biomass collection as little as possible, and since experimental treatments (fertilization and additional illumination) affected an area considerably larger than 40×40 cm (ca 1 m²), it was reasonable to place the centers of subplots at the four corners of each permanent plot.

Above-ground biomass of plants rooted in a subplot was harvested by canopy strata 4 cm deep and sorted according to basic morphology (four growth-form classes: grasses, sedges, upright- and rosette forbs; Liira and Zobel 2000). All biomass samples were dried at 75° C for 24 h and weighed. For analysis, we used biomass density data (biomass samples from 4 cm layers; volume 201 cm³; IV).

Permanent plot study 2 (Paper III)

An additional field study was carried out in Laelatu wooded meadow in 2004–2005 (III). 80 circular subplots (diameter 10 cm) were centered regularly into the corners of 20 40 × 40 cm permanent plots, which were placed randomly across an area of ca 500 m². The number of plant ramets was counted and species identified for each ramet rooted in a sub-plot four times a year – from Mid-May to late July in both study years (altogether 8 times).

2.3. Inter-community study of community structure and diversity

We used data from 17 herbaceous communities in Estonia to test our hypotheses at a large-scale (II). These communities, exhibiting contrasting productivity and diversity, were selected from communities investigated in 1994–1995 by Zobel and Liira (Tables 1 and 2 in Zobel and Liira 1997; for more detailed description of the methods see Zobel and Liira 1997 and Paper II). We chose communities in which more than 10% of the species found in the community species pool were grown in the garden experiment (Table 1, S1 in II). The selected study areas were either grasslands or forest field layer communities. All communities were dominated by perennials.

Community species pools were defined as all species found in each entire community. The spatial variability of canopy height was estimated using point quadrat analysis. A 3-mm metal pin was inserted through the herbaceous canopy

at randomly chosen locations within a 10×10 m seemingly homogenous plot. The heights at which the pin made contacts with the green foliage and stems of plants were recorded. Pin insertion was recorded only when the pin touched a green plant at least once. The coefficient of variation of mean canopy height was calculated as the standard deviation of mean heights of contacts on a pin, divided by the overall mean of heights of contacts across all pins.

In each of the 17 communities, additional biomass and diversity parameters were measured inside the same 10 × 10 m plot. At all study sites three randomly positioned flexible-size quadrats were also examined; the quadrats were re-sized to contain 500 vascular plant ramets (area measured with the precision of 0.5 cm²), all species were recorded, and standing biomass was harvested, dried and weighed. Also, a quadrat of 1 m² in one corner of the 10×10 m plot was floristically described.

For each community the following characteristics were estimated as the mean of three replicates: ramet biomass (the mean size of one plant ramet), ramet density (the number of plant ramets per unit area), relative richness per 1 m² (the proportion of the community species pool found in 1 m²) and relative richness per 500 ramets (the proportion of the community species pool found in 500 adjacent ramets). Only relative richness measures were used in the statistical analysis. This is due to the fact that most of the variation in small-scale richness across communities is described by the size of community species pool (Zobel and Liira 1997) and the possible effect of shoot plasticity would be obscured in absolute richness measures.

2.4. Data analysis

Using plasticity estimates for studied species, species lists from permanent plots and data from 17 herbaceous communities, we calculated the average plasticity of species present at each studied site. We calculated average species shoot plasticity (Π ; **II**) and average species leaf area plasticity (Π_{LA} ; **III**) per plot as the average across the species for which we had plasticity estimated in a garden experiment. A similar calculation of species mean shoot plasticity (Π) was carried out for the 17 studied grassland communities – calculated as the average across those species registered in three replicate 500-ramet plots, for which the shoot plasticity estimate was known (**II**). These average plasticity estimates were used in further analyses to describe the degree of plasticity of species growing in a given assemblage or community.

Statistical analyses. Paper I

The general pattern of change in plant growth in response to shading across all studied species was analyzed using random intercept linear mixed models that included light availability as a fixed factor with four levels and species as random factor. We compared each full model to a reduced model not containing

light availability using a likelihood ratio test to estimate the significance of the shading effects. Data analyses were performed using R 2.11.1 (R Development Core Team 2010). Mixed models were implemented using R packages nlme (Pinheiro et al. 2009) and lme4 (Bates et al. 2011).

Statistical analyses. Paper **II**

We used General Linear models (GLM) to describe the effects of plant species mean height, Ellenberg indicator values for light and for nutrients, leaf width (two levels) and presence/absence of leafy stem (two levels), on the shoot plasticity of species.

The overall effect of mean species plasticity on species richness was tested using GLM with year included as a random factor. The effect of mean species shoot plasticity on local species richness was also tested separately for five consecutive years using linear regression analysis. Relationships between mean species plasticity and community characteristics over 17 grassland sites were studied using GLM. Data were analyzed using Statistica software (Statistica 6.0; StaSoft Inc., Tulsa USA).

Statistical analyses. Paper **III**

The effect of mean shoot plasticity and ramet density on small-scale species richness was tested using a mixed GLM, with the random factor “plot” included in the model and factor “subplot” nested in “plot”. Data were analyzed using Statistica software (Statistica 6.0; StaSoft Inc., Tulsa USA).

Statistical analyses. Paper **IV**

ANOVA was used to examine the effects of different treatments, canopy layer and growth form on above-ground biomass density in a subplot. Plot was included into all models as a random factor. Data was analyzed using Statistica software (Statistica 6.0; StaSoft Inc., Tulsa USA).

3. RESULTS

3.1. Plasticity and other basic traits of the studied species

The shading treatments had a critical, although rather unexpected effect on plant growth. Averaged across the 46 studied species, plant dry mass was highest among plants grown in 50% shade (Fig. 1 in **I**). The relative difference in mean plant dry mass between the 50% of daylight and full daylight treatments was mostly positive. Still some species attained similar or less dry mass in moderate shade than in full daylight (Fig. 2 and Table S2 in **I**). Variation in growth response to shading was significantly related to species synecological demands (Ellenberg's nitrogen and moisture values). Species typical of less fertile and dry habitats exhibited the greatest increase in dry mass in 50% shade compared with full daylight (Fig. 3 in **I**). Some plant species even attained higher biomass growing in 90% shade than in full-light conditions (Table S2 in **I**). Species that attained similar or less biomass in 50% shade than in full daylight were effectively increasing allocation to leaf area (LAR) and relatively higher allocation to root biomass in the moderate shade treatment (Fig. 3 in **I**). The growth of species exhibiting low LAR plasticity or even increased allocation to leaf area with increasing light availability was clearly facilitated by shading (Fig. 4 in **I**).

None of species mean height, species light or nutrient demand showed a significant relationship with experimentally estimated size-independent shoot plasticity to light availability (**II**). The shoot plasticities of species with contrasting basic morphology (narrow vs wide leaves and presence vs absence of leafy stem; grasses, sedges, upright forbs and rosette-forming forbs) were not significantly different (**II**).

3.2. The effect of plasticity on community structure and diversity

The number of herbaceous species in permanent plots on a calcareous wooded meadow was positively related to mean local shoot plasticity (Table 4, Fig. 3 in **II**) and the mean leaf area plasticity (Table 1, Fig. 1 in **III**) of co-existing species. This means that species diversity in local assemblages was higher when there was a high concentration of plastic species. Species richness per unit area was consistently and closely dependent on the local density of plants (ramet density; Fig. 2 in **II**, Fig. 2 in **III**). However, the link between morphological plasticity and species diversity was not mediated only by higher ramet density in plastic plant assemblages in Laelatu meadow (Table 1 in **III**).

The inter-community study showed that mean shoot plasticity was related to the spatial distribution of plant biomass in 17 grassland communities. In communities with relatively high average shoot plasticity, the variability of

herbaceous canopy height was significantly lower, indicating reduced competition asymmetry of co-existing species (Table 3 and Fig. 1D in **II**). Further analysis revealed that at this relationship was not mediated by ramet density; in a model where both ramet density and plasticity were included as independent variables, only the latter was significantly related to canopy height variability (Table 3 in **II**).

Among the 17 studied communities, ramet density was positively related to mean species shoot plasticity as well as to ramet biomass (Table 2, Fig. 1A in **II**). On the other hand, ramet density was a good predictor of relative richness per square meter (Table 3, Fig. 2 in **II**). A larger proportion of the community species pool was represented in 1 m² plots in communities with denser vegetation. Given these two relationships, it was not surprising that the estimate of mean species plasticity was positively related to relative richness per unit area (Table 2, Fig. 1B in **II**). This relationship probably reflects the fact that communities of plastic plants allow denser canopies – there was no relationship between plasticity and relative richness per 500 ramets (density independent estimate of relative richness; Tables 2, 3 and Fig. 1C in **II**).

In experimentally manipulated permanent plots, above-ground biomass density across all species (in a 4 cm canopy layer) was not significantly changed by artificial light addition although a significant shift in biomass vertical distribution was detected (Table 4 in **IV**). On the contrary, nutrient addition increased biomass density while biomass density distribution was retained (Table 4 in **IV**). The biomass density of species with contrasting basic morphology was differently affected by light addition. Enhanced light intensity significantly increased the biomass density of species with narrow leaves (graminoids) in the lower part of the canopy, while other growth forms (forbs) showed a certain but statistically non-significant decrease (Table 1, Fig. 2 in **IV**).

4. DISCUSSION

Our studies show that in temperate grasslands acclimatization to the light-environment is expressed both through size-dependent plasticity (**I**) and size-independent plastic reactions (**II**; **III**). Both are important for developing different aspects of species acclimatization and thus community formation. Although both acclimatization strategies are triggered by light availability, contrasting growth trajectories are associated with adaptation to different habitat resource levels (**I**), while size-independent plasticity to light is related to a plant's strategy of coping with its neighboring ramet in an assemblage (**II**, **III**; see also Ackerly and Cornwell 2007).

The results of a garden experiment indicate clearly that for many species growing in a surplus of below-ground resources, an absence of shade does not promote fastest growth. Although most plants grew significantly larger in shade, a wide variety of growth responses to light availability were detected (Figs 1 and 2 in **I**). Size-related morphological acclimatization was connected with species synecological optima for nutrient and water availability. Species adapted to infertile conditions were somewhat surprisingly more facilitated by shade, showing faster growth, and investing less resources into leaf area and shoot biomass, when grown in half-shade (Fig. 2 in **I**). Such reduced growth in full-light conditions could be caused by high investment of resources into the tolerance of abiotic stress, resistance to herbivore and pathogen attack etc. (the cost of physiological acclimatization or active down-regulation of growth; Dudley and Schmitt 1996, Rose et al. 2009, Feng et al. 2009). Reduced allocation into leaf area in low light conditions represents an opposite reaction to the morphological plasticity for attaining optimal biomass partitioning in light deficiency that is usually recorded. This reaction probably indicates a close allometric dependence between the studied traits and biomass – an alternative mechanism for acclimatization (McConnaughay and Coleman 1999; in a narrower sense it may not be considered “true” plasticity at all, but see Gianoli and Valladares 2012). In this case, morphological adaptations to light in low-productivity species are directly dependent on plant biomass (Bell and Galloway 2007).

At the other end of the growth-response gradient there are species adapted to resource-rich habitats, whose acclimatization responses to shaded conditions are close to the optimal partition principle (McConnaughay and Coleman 1999; Fig. 3 in **I**). Species that produce more or less similar biomass in full light and 50% shade, showed significantly increased allocation to root biomass in high light and allocation to leaf area in moderate shade (Fig. 2 in **I**). This indicates a somewhat different relationship between plant morphology and growth (plasticity) than exhibited by shade-facilitated species. The result of higher size-related morphological plasticity in species from productive habitats was not in accordance with our results on size-independent morphological plasticity presented in Paper **II**. This supports the notion that these two studies evaluate

separate components of acclimation ability. The above-described gradient of size-related light-acclimatization shapes the potential of species to grow in conditions of varying below-ground resource availability. Species adapted to resource-poor conditions can be strongly facilitated by neighboring shade, indicating the importance of positive interactions for successful growth in such conditions. On the other hand, species coming from conditions of high below-ground resource availability are adapted to partition biomass optimally for light acquisition, depending on local light availability levels. Surrounding luxuriant vegetation in high-resource conditions is supposedly reduces the risk and severity of herbivory, which has been shown to cause serious damage, especially for rapidly growing plants (Rose et al. 2009).

Experimentally estimated size-independent plasticity to light availability (S1 in **II**) was not significantly related with any studied plant characteristics – growth, basic morphology or resource-requirement (**II**). Nonetheless it exerts a remarkable effect on community structure (**II**, **III**). Shoot plasticity had a consistent effect on the performance of plant species in natural grassland assemblages and played a significant role in structuring communities. Herbaceous communities containing species with high average shoot plasticity to light availability were far more diverse (**II**, **III**). This positive relationship between plasticity and species number was consistent over years and was detected at the local scale (Fig. 3 in **II**; Fig. 1 in **III**) as well as in inter-community comparisons (Fig. 1 in **II**).

The simplest interpretation of the positive relationship between plasticity and diversity is through the number of locally co-existing ramets per unit area (Fisher et al. 1943, Oksanen 1996). It is reasonable to assume that ramet density would be an important factor governing species richness per unit area (Table 2 and 3, Fig. 2 in **II**; Table 1, Fig. 2 in **III**). The higher the ramet density, and consequently the number of individuals studied, the higher is species diversity in a plot. However, the relationship between plasticity and ramet density appears to be more complex. The effect of species mean plasticity on local diversity is evidently mediated by ramet density at the large scale (**II**), but at the local scale the “concentration of plasticity” has a direct density-independent positive effect on richness (Table 1 in **III**).

One possible reason for the observed positive relationship between ramet density and plasticity in the inter-community study (Table 2 and 3, Fig. 2 in **II**) could be the widely assumed relationship between morphological plasticity and the competitive strategy of species, acting as an *equalizing force* that reduces fitness differences between species; Chesson 2000, Wenekes et al. 2012). Phenotypic plasticity has been shown to lower competition intensity (Schmitt et al. 1995, van Kleunen and Fisher 2001, Vermeulen et al. 2008) and reduce competition asymmetry (Schwinnig and Weiner 1998, Aphalo et al. 1999, Stoll et al. 2002, Vermeulen et al. 2008, **II**). By increasing or restricting elongation, depending on the start-position of ramets, plastic acclimatization has been shown to result in nearly even vertical growth in a stand (Nagashima and

Hikosaka 2011). More symmetrical above-ground competition between plastic species, as indicated by the decreased variation in plant height, could also be one mechanism behind the significantly higher ramet density in high-plasticity communities (Table 2 and 3, Fig. 1 in **II**; Aphalo et al. 1999, Stoll et al. 2002).

The elongation of shaded plastic individuals should result in a smaller plant unit area (area occupied by one plant ramet; Schwinnig and Weiner 1998 and references therein) and allow for more ramets to occupy a fixed area. In those microsites where plastic species prevail, all species in the local assembly would benefit from the possibility of growing extra shoots (Table 3, Fig. 1 in **II**). If changes in the numbers of individuals is independent of species identity, this would explain why the proportion of the community species pool detected amongst 500 adjacent ramets does not depend on species average plasticity (Fig. 1, Table 2 in **II**). Neutral selection of species into assemblages should result in the relative species diversity per ramet to be a more or less constant proportion of community species pool. Earlier studies performed in the same communities indicate that this could be the case here (Zobel and Liira 1997).

If we look at the same problem within one grassland community, the results show a different pattern (**III**; indicating *stabilizing forces*, making species limit themselves more than others; Chesson 2000; Wennekes 2012). One possible mechanism underlying the high diversity per ramet independent of ramet density observed in plots with high average plasticity (**III**) could possibly be shade avoidance syndrome. Plants growing in shade often exhibit elongated growth with taller stems, longer petioles and increased SLA, but also demonstrate remarkable self-restraint through slender vertical leaves and suppressed branching, resulting in fewer stems (Schwinnig and Weiner 1998, Maddonni et al. 2002, Franklin 2008, Leyser 2009, Keuskamp et al. 2010, Skålovà 2010, Pierik et al. 2012). When species with high shoot plasticity are growing nearby, the plastic reaction to neighboring shade can result in decreased vegetative sprouting and therefore in lower ramet number per genet (Skålovà 2010). At the scale of local assemblages this may result in higher diversity per ramet in the case of plastic species (**III**) if the community species pool is large enough. When there is reduced tillering, ramet density can be lower without a loss of species diversity per unit area (since there is no need for exclusions of genets in this scenario).

It could be speculated here that the nature of the effect of plasticity on local diversity depends on the scale and appears to operate through two different mechanisms. Our preliminary analysis indicates that at the inter-community scale plasticity probably reduces competitive exclusion through more equal growth and resource partitioning (*equalizing forces*). Within a single community, self-restraint of individuals (*stabilizing forces*) seems to be more important. However, the generality of the relationships between plasticity, diversity and species density remains to be established in future studies.

In the permanent plot study with light and nutrient addition as experimental manipulations, we learned that moderate and local improvement in resource

availability (in **II** and **IV**) had no significant effect on species composition (Eek and Zobel 2001, see also Liira et al. 2012). Therefore it was possible to study the effect of resource availability on community structure without confusing changes in species composition. The previous results of the five-year experiment suggest that there is no significant light-limitation in the herbaceous layer of this wooded meadow (Urbas and Zobel 2000, Eek and Zobel 2001). However, the effect of plasticity to light availability on species morphology, and therefore community structure, was clearly detectable (**IV**). Light availability caused changes in the vertical distribution of biomass, while average biomass density was left unaffected (Table 4 in **IV**), resulting in changes of the vertical light gradient in the canopy (Rajaniemi 2002). Our autecological study revealed that plants growth is the fastest in moderately shaded conditions (Fig. 1 in **I**) and affirmed that plastic arrangements in morphology are not intrinsically associated with biomass (**I**, **II**). Plastic adjustments in plant architecture are supposed to result in a more even biomass distribution among plants and an increase of resource-use complementarity (Callaway et al. 2003, Wacker et al. 2009), probably through character displacement in light deficiency. In artificially improved light conditions this kind of coordination was not necessary and thence the different biomass vertical distribution in plots with artificial light addition (Table 4 in **IV**). Nutrient addition had the opposite effect – biomass density increased while vertical distribution of biomass was stable (Table 4 in **IV**) possibly alluding to inevitable changes in growth-rate (Aerts et al. 1991, Janeček et al., 2013).

Species with contrasting leaf width showed opposite reactions to light addition: graminoids significantly increased their biomass density while forbs decreased it (although statistically non-significantly; Fig. 2B in **IV**). Size-independent shoot plasticity, estimated in the garden experiment, showed no difference between growth-forms (**II**), indicating that those arrangements were made through some other mechanisms.

All changes in community vertical structure occurred through phenotypic changes (including plasticity) and without considerable shifts in species composition. The zero effect of experimental manipulations on species composition allow me to propose that the observed relationships between diversity, density and size-independent plasticity were not results of inevitable responses to general resource availability, but probably the outcome of adaptive plastic reactions to local light climate (de Kroon et al. 2005) resulting in shifts of community structure and diversity (**II**, **III**, **IV**).

5. CONCLUSIONS

The results presented in this thesis indicate that size-related and size-independent plastic reactions to light availability influence different aspects of species acclimatization and community structure (**I**, **II**, **III**, **IV**). Size-related morphological acclimatization is connected with species nutrient requirements. Species adapted with resource-poor conditions show strong facilitation by moderate shade, resulting in markedly better growth in such conditions. Adaptation to high below-ground resource availability was coupled with acclimatization to local light availability, matching the predictions of the optimal partitioning principle. This presumably plastic response led to near equal growth in full light and moderately shaded conditions. Nevertheless, there were no detectable relationships between size-independent plasticity and other studied characteristics of species under examination (resource requirements, growth-form or height; **II**).

Experimentally estimated size-independent plasticity to light availability has a strong effect on community structure (**II**, **III**). Herbaceous communities containing species with high average plasticity to light were far more diverse (**II**, **III**). This positive relationship between plasticity and species number was consistent in time and was detected both in intra- and inter-community comparisons (**II**, **III**). More symmetrical above-ground competition between plastic species could be one of the reasons why less competitive exclusion occurs in communities with significantly higher ramet density and diversity per unit area (**II**). Still, the proportion of the community species pool detected amongst 500 adjacent ramets was not dependent on species average plasticity (**II**). At the local scale, the relationship between plasticity and species richness was not (at least entirely) mediated by the density of individuals (**III**) and it was possible to detect a direct effect of plasticity on diversity (**III**).

Moderate experimental changes in resource-availabilities had significant effect on community biomass density (below-ground resource addition) and vertical distribution of biomass density (light-resource addition), responses being clearly growth-form specific (**IV**). Plastic adjustments of plant architecture probably result in increased resource-use complementarity without considerable shift in species composition (**IV**).

Previous studies have revealed that there is no direct link between herbaceous species diversity and moderately increased resource availability in the Laelatu wooded meadow. We showed that average plasticity of co-growing species has a remarkable effect on diversity (**II**, **III**). Therefore I propose that, at least in our study-system, plant growth and survival in an assemblage mainly depends on direct interactions with immediate neighbours and not so much on local heterogeneity in resource availability. Although there is already a wide range of theories and available evidence concerning the persistence of high diversity plant communities, we propose that high size-independent phenotypic plasticity to light should be recognized as one “way” for forming dense and diverse plant assemblages.

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SUMMARY IN ESTONIAN

Valguse kättesaadavuse mõju rohttaimede kasvule ning avaldunud liigiomase plastilisuse roll niidukoosluste struktuuri ja liigirikkuse kujunemisel

Taimedel kui sessiilsetel organismidel on eluliselt oluline ja laialt levinud omadus geneetiliselt määratud aklimatsioonivõime e fenotüüpne plastilisus. Ainuüksi põgusal tutvumisel, olgu vaadeldavateks potililled või niidukooslus, hakkab silma taimede märkimisväärne suutlikkus oma ehitust keskkonnatingimustele vastavaks kohandada (morfoloogiline plastilisus). Kõigi roheliste taimede ühise ressursi – päikesevalguse (täpsemalt fotosünteesiliselt aktiivse kiirguse) – vajalikul tasemel omastamiseks on taimedel kasutusel hulgaliselt strateegiaid. Naaberisendite varjus kasvavad taimed enamasti kõrgemaks ja saledamaks, lehtede (suhteline) pindala on suurem, lehed on õhemad ja püstisemad, taimed harunevad vähem jms. Valgustingimuste muutustega kohanemise tagajärjel tekkivaid muutusi morfoloogias esineb sõltuvalt taime liigiomadustest (kasvuvorm, ehituslaad, ressursinõudlus, elukäiguomadused) ning biotilistest ja abiotilistest keskkonnaparametritest lõputuis kombinatsioonides.

Lähestikku kasvavate isendite lehtede ja varte asetuse, suuruse ning kuju vastastikuse sobitamise teel on võimalik taimedel märkimisväärselt muuta võsudevahelist mõju, selle suunda ja tugevust. Muutused taime morfoloogias saavad põhimõtteliselt asendada kuluka agressiivse konkurentsivõitluse oluliste kahjulike mõjudeta kooseksisteerimise või koguni teineteise kasvu soosiva suhtega. Just seetõttu on alust arvata, et plastiline kohanemisvõime mõjutab märkimisväärselt taimekoosluste struktuuri kujunemist. Taimede morfoloogiline plastilisus ja selle mõju koosluste struktuurile on olnud taimeökoloogide huvi-orbiidis juba enam kui sada aastat. Võimalik, et peamiselt sobiliku meetoodika puudumise tõttu on plastilisuse rolli uurimine jäänud matemaatiliste mudelite, teooriate ja mõneliigiliste kunstlike koosluste analüüsimise juurde. Kasutades plastilisuse hindamisel nii klassikalist lähenemisnurka kui ka uudsemat meetoodikat, on käesoleva doktoritöö peamiseks sihiks uurida hinnangute paikapidavust reaalses paljuliigilises koosluses.

Minu doktoritöö peamised eesmärgid olid järgmised.

1. Saada adekvaatseid ja võrreldavaid võsu morfoloogilise plastilisuse eksperimentaalseid hinnanguid esindava hulga rohttaimeliikide jaoks (**II**). Samuti selgitada, kuidas on liikide plastilisus valguse suhtes seotud teiste põhiliste liigiomadustega (kõrguskasv, sünökoloogilised ressursinõudlused, kasvuvorm jm), kasutades nii taimesuurusel sõltuvaid (**I**) kui sõltumatuid plastilisuse hinnanguid (**II**).

2. Selgitada, kuidas mõjutab kooseksisteerivate taimede suurusest sõltumatu plastilisus valguse suhtes rohttaimekoosluste struktuuri ja liigilist mitmekesisust (**II, III**).
3. Saada teada, kuidas mõjutab mõõdukas ressursitaseme muutus niidukoosluse vertikaalset struktuuri ning kui võrd sõltub eksperimentaalsete töötluste mõju võsude biomassi tihedusele taimede kasvuvormist (**IV**).

Taimede morfoloogilise kohanemise uurimiseks kasvatasime katseaias täisvalguses ja erineva varjutihedusega telkides (50%, 25% või 10% päikesevalgusest) 46 liiki kuuluvaid Eesti kooslustes levinud rohttaimi (**I, II, III**). Peale 10-nädalast kasvumist mõõdukalt väetatud ning optimaalse niiskuse režiimi tingimustes taimed koguti, kuivatati ja mõõdistati hulk morfoloogilisi tunnuseid (lehtede pindala, lehtede arv, kogukaal, lehtede kaal jne). Mõõdetud tunnuse väärtuste põhjal analüüsisime kõigi liikide lehetunnuste ja kasvu erinevusi valgusgradiendil ning hindasime kahe meetodika alusel lehetunnuste plastilisuse.

Suurusega seotud plastilisuse hindamiseks arvutati iga liigi jaoks tunnuse väärtuse suhteline erinevus täisvalguses ja poolvarjus (lehepinna osakaal, lehtede eripind, juurte osakaal; **I**). Sarnaselt hinnati ka taimede biomassi suhtelist erinevust, kirjeldamaks taimede kasvuerinevusi sõltuvalt valguse kättesaadavusest (**I**).

Taimeliigi suurusest sõltumatu plastilisuse kindlakstegemiseks leidsin tunnuse keskkonnast tingitud plastilise kohanemise ulatuse e reaktsiooninormi tõusunurga, eemaldades samas taimesuuruse allomeetrilise mõju tunnuse väärtusele. Selleks koostasid üldistatud lineaarse mudeli, kus sõltuvaks faktoriks oli uuritava tunnuse logaritmitud väärtus (lehtede keskmine pindala või lehtede arv) ja sõltumatuteks faktoriteks valguse kättesaadavusprotsent ning tunnuse väärtust oluliselt mõjutavad biomassi teisendused. Saadud mudelis kirjeldab valguse kättesaadavuse parameetri hinnang uuritava tunnuse reaktsiooninormi tõusu, mis sedasi arvutatuna võimaldab võrrelda omavahel nii eri liikide kui ka tunnuste plastilisust. Kasutades kirjandusest saadud andmeid taimeliikide sünökoloogiliste ressursinõudluste kohta (Ellenbergi väärtarvud), katses määratud taimeliikide keskmist kõrgust täisvalguses ning kasvuvormi, uurisime nende omaduste seoseid katseliselt kindlaks tehtud plastilisuse hinnangutega (**I, II**).

Suurusest sõltumatu plastilisuse võimalikku mõju taimekooslusesisese struktuuri kujunemisele uurisime Laelatu puisniidul. Selleks tegime kindlaks kahe erineva suurusega püsiruutude taimestiku liiginimekirjad, suurematel püsiruutudel viiel järjekorras aastal ja väiksematel kahe aasta lõikes (**II, III**). Väiksematel prooviruutudel loendasime kõigil vaatluskordadel ka rametite arvu (**III**).

Samas koosluses uurisime ka ressursitasemete toimet taimestiku vertikaalsele ja kasvuvormilisele struktuurile. Viie aasta jooksul katseliselt suurendatud toitainete ja päikesevalguse kättesaadavuse mõju hindamiseks kogusime püsiruutudel juurdunud taimede maapealset biomassi 4 cm kihtidena ning kaalusime

kuivbiomassi kasvuvormide kaupa (kõrrelised, tarnad, püstised ja rosetjad rohunid; **IV**).

Erinevate koosluste omavaheliseks võrdlemiseks kasutasime andmeid Zobeli ja Liira (2000a) uurimusest (**II**). Eestimaa eri paikades asuvates 17 rohttaimekoosluses mõõdeti rametite tihedus, liikide arv 500 rameti kohta ning 1 m² prooviruudul, koosluse liigifondi suurus ning produktsioon (valisime välja need kooslused, kus kasvanud liikidest enam kui 10% jaoks oli plastilisus katseliselt hinnatud). Samades kooslustes hinnati ka nõelameetodil rohttaimede võra kõrguse varieeruvust. Koostatud liiginimekirjade põhjal arvutasime kõigi prooviruutude jaoks seal kasvavate taimeliikide keskmised suurusest sõltumatud plastilisuse määrad (**II, III**) ning analüüsisime keskmise plastilisuse ning koosluse parameetrite omavahelisi statistilisi seoseid.

Selgus, et katseaias poolvarjus hoitud taimede kasv oli teistes tingimustes kasvanute keskmisest oluliselt kiirem (**I**). Eriti soodsalt mõjus mõõdukas vari toitainevaeste ja kuivade tingimustega kohastunud liikide kasvule, hoolimata sellest, et nende reaktsioon varjutamisele oli optimaalseks peetavale vastupidine (näiteks oli lehepinna osakaal varjus väiksem). Ilmselt muudab naabertaimede vari keskkonningimused soodsamaks eeskätt väheviljakate kasvukohtade liikide jaoks. Taimede kasvu hästivalgustatud hõredas väheviljakas koosluses pärsivad oluliselt kasvamiseks vajalikud ning ilmselt kulukad füsioloogilised kohastumused valgustressi ja võimaliku herbivooria mõju vähendamiseks. Seevastu produktiivsemate tingimustega kohastunud liikide morfoloogiline reaktsioon varjutamisele oli optimaalseks peetavale lähedane ning nende taimede kasv täisvalguses ja poolvarjus oli pea võrdne (**I**). Kuigi selline kohanemine peaks olema võimalik eeskätt läbi suurema morfoloogilise plastilisuse, ei olnud nende samade taimede suurusevaba plastilisuse hinnang seotud ühegi uuritud taime omadusega (ressursinõudlused, kasvuvorm, kõrguskasv; **II**).

Ilmnes, et rohttaimede liigirikkus pindalühiku kohta oli oluliselt kõrgem neil uurimisaladel, kus kasvasid koos suure morfoloogilise plastilisusega liigid (**II, III**). Seos oli vaadeldav nii koosluste võrdluses kui ka kooslusesiseselt ning püsis samasuunaline nii aasta lõikes kui ka üle aastate, olenemata püsiruudu suurusest. Ainuüksi matemaatilistel põhjustel on pindalapõhise liigirikkuse olulisimaks määrajaks nii koosluse sees kui ka koosluste omavahelises võrdluses vaadeldud isendite arv e rametite tihedus prooviruudul (**II, III**).

Eri kooslustest kogutud andmete kõrvutamisel selgus, et keskmisest plastilisemate liikide kooskasvamisel on taimekoosluses võsude kõrgusvarieeruvus oluliselt väiksem ning rametite tihedus suurem (**II**). On tõenäoline, et suurem võsude tihedus ühtlasema kõrguskasvuga taimekooslustes on vähemalt osalt võimalik tänu pidurdunud konkurentsele väljatõrjumisele naaberisendite varjust hoiduvate plastiliste liikide kooskasvamisel. Seeläbi saavutatud suurem isendite arv pindala kohta toob kaasa ka kõrgema liigirikkuse prooviruudul. Samas ei mänginud taimeliikide üldine valgustingimustega kohanemise võime koosluste liigitiheduse (liikide arv ühe võsu kohta) määramisel mingit rolli, vihjates neutraalsetele protsessidele võsude tiheduse kujunemisel (**II**).

Ühe koosluse piires (Laelatu puisniit) olid plastilisuse määra ja liigirikkuse seosed mõnevõrra teistsugused. Nagu kooslustevahelises võrdluseski oli keskmiselt suurema plastilisusega liikide kooskasvamisel kohalik liigirikkus suurem. Erinevalt kooslustevahelisest võrdlusest jäi plastilisuse mõju liigirikkusele statistiliselt oluliseks ka siis, kui mudelisse lülitati võsude tihedus kui otseselt pindalapõhist liigirikkust mõjutav tegur (**III**). Saadud tulemused vihjavad lähemat uurimist väärivale võimalusele, et Laelatu rohttaimekoosluse struktuuri kujunemisel on lisaks konkurentse väljatõrjumise vähenemisele ja valguskeskkonnaga kohanemise edukusele oluline ka taimede morfoloogilise „enesepiiramise” võime. Valguse pärast konkureerivate struktuuride tiheduse vähendamine läbi väiksema harunemise ja vegetatiivse paljunemise võimaldab vältida konkurentsipinget liigset tugevnemist ja seeläbi suurenevat väljatõrjumise tõenäosust.

Kuigi eksperimentaalselt suurendatud toitainete ja valguse kättesaadavus Laelatu puisniidul liigirikkust ei mõjutanud, ilmnes oluline ressursitaseme mõju koosluse biomassi tihedusjaotusele. Valguse kättesaadavus mõjutas oluliselt niiduliikide biomassi paigutust võras (**IV**). Koosluse lisaväetamine seevastu suurendas oluliselt rohurinde biomassi tihedust, jättes biomassi vertikaalse jaotuse samaks (**IV**). Kasvuvormiti oli biomassi tiheduse reaktsioon keskkonna ressursitaseme muutmisele erinev (**IV**).

Varasemad uuringud Laelatu puisniidule rajatud katsealal ei leidnud otsest seost rohurinde liigirikkuse ja mõõdukalt suurendatud ressursitasemete vahel, samas kui käesolevas töös on kirjeldatud plastilise kohanemise võime märkimisväärt mõju koosluse kujunemisele. Antud tulemuste kõrvutamine võimaldab mul järeldada, et selle rohumaa liigilise koosseisu kujunemisel on eelkõige määravaks kooskasvavate isendite plastiline lähinaabrite arhitektuuriga kohanemise võime, mitte ressursside kättesaadavuse mõõdukas varieerumine (**II**, **III**).

Minu doktoritöös esitatud uurimistulemused näitavad, et rohttaimede suurusel sõltumatu plastilisus valguse suhtes on liigiomadus, mis otseselt ja oluliselt mõjutab parasvöötme rohumaa struktuuri ja liigirikkuse kujunemist. Kooselavate liikide aktiivne ja eeldatavalt adaptiivne plastilisus on üheks tingimuseks liigirohkete koosluste tekkeks ja püsimiseks.

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