Vegetation-Environment Relationship in Estonian *Hepatica* Site Type Forests in the Light of A. K. Cajander's Forest Site Type Approach

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Paal, J., Rajandu, E. and Köster, T. 2010. Vegetation-Environment Relationship in Estonian *Hepatica* Site Type Forests in the Light of A. K. Cajander's Forest Site Type Approach. *Baltic Forestry* 16 (2): 194–208.

Abstract

In many countries, including Estonia, the interpretation of forest vegetation-environment relationship and forest typology proceeds from A. K. Cajander's site type concept. It presumes that the environmental conditions of habitats, the tree layer productivity of forests, and ground vegetation composition are well correlated, whereas the tree layer composition may develop rather independently. We studied (i) how uniform are the soil conditions within the limits of Estonian mesic *Hepatica* forest site type communities, (ii) how similar the species content of these forests is in different districts, (iii) how the species content similarity is expressed in the different layers of forest communities and, (iv) which environmental factors determine the species richness most essentially. One study area was situated in western Estonia on calcareous soils lying on bedrock limestone, two areas in southern Estonia on parent material with variable calcareousness. The soils of these areas differ remarkably by their morphology and by their chemical properties. The average species richness of vascular plants and bryophyte species in all three areas appeared to be rather similar. The diversity of herb layer species was positively affected only by the habitat lightness, while we did not discover any analysed environmental variable for the moss layer, which had significant effect on the species richness. The species composition in forests of the three study areas differs significantly for the moss, herb and bush layer. For every forest community layer its own system of relationships between the species as well as between the species and environmental factors is characteristic. The relative autonomy of plant community layers is in good accordance with Cajander's theory of forest site types. In western Estonia the height of trees, the diameter of stems and the timber volume are essentially lower than in southern Estonia due to the dryer soils. Therefore, it seems relevant to divide the Estonian *Hepatica* site type forests into two subtypes: the first is confined to calcareous soils in the western and northern Estonia and has lower habitat productivity potential for tree layer in comparison with the forests of the second subtype that grow mostly in the eastern and southern Estonia on soils mainly depending on the topographical location and parent material calcareousness but having a higher tree layer productivity.

Key words: Cajander, classification, layers, management, productivity, site type, soils, species richness, stand age, trees growth

Introduction

Study of relationships between the vegetation and the environment has been the main issue of plant communities' ecology from its beginning and the respective general regularities are rather well known. Nevertheless, depending on the scale, involved characters, region and communities under study, there is a multitude of peculiarities and variations having often a crucial importance for management planning and implementation. Circumstantial understanding of them is a reliable basis for more successful results, which is especially obvious in forestry practice. Sound planning in forestry is site-specific but arranged generally according to the forest site types. Therefore the efficiency of forestry depends largely on how well the conditions and features of every site type in the considered region are known.

In numerous countries, the forest site types are distinguished and delimited according to the concept developed mainly by A.K.Cajander (1909, 1926, 1930, 1949, Cajander and Ilvessalo 1921). In Estonian forest typology Cajander's approach was introduced already in the 1930s by Rühl (1932, 1936) and developed further by Ilves (1953), Karu and Muiste (1958), Katus and Tappo (1965) and Masing (1966, 1969). The forest site type ordination scheme elaborated by Lõhmus (1974a,b, 2004) and accepted for several decades as an official guideline of the Estonian forest inventory and management planning, is closely related to the same concept as well.

Cajander's forest site type approach proceeds from the presumption that between the habitat/site conditions, forest communities tree layer growth/productivity and ground vegetation species composition a rather strong correlation exists, whereas the tree layer composition may develop relatively independently, first of all due to the human interference or fires. In that way, the mapping of forest vegetation communities can also provide an overview or even map of forest soils (Cajander 1923, 1930, 1949, Kalela 1960). Still, as it has been demonstrated by several authors, the relationship between different components of forest communities' structure and habitat properties is often rather weak (e.g. Василевич and Константинова 1980). In different regions and in different communities relationships between the vegetation and habitat characteristics usually have their own peculiarities. In the Kivach Nature Reserve, located in the middle taiga zone of Russian Karelia, for example, the forests ground vegetation, tree layer and soil properties classifications had a good consonance (p = 0.001; Paal 1995), while for the forests in the Karula National Park, South Estonia, these classifications did not have any acceptable correspondence (Vellak et al. 2003). It has been established also that dynamics of different components in the ecosystems is non-synchronous. According to Таргулян and Соколов (1978) the soil and vegetation have different ‚characteristic time', i.e. a period in the course of which they will attain a state of relative equilibrium. This period can be different already for the particular soil properties. Moreover, the relations between plant communities' components and environmental parameters can be subjected to some independent factors like soil parent material or climate not considered in the analysis.

Since Cajander's approach was mainly designed for and is continuously used in practical forestry, only a modest number of distinct site types for certain region can be applicable (Cajander 1949). At the same time, the diversity of forest habitat conditions and vegetation characteristics is frequently very large and continuously changing; therefore it is complicated to describe it in terms of a restricted number of habitat site types (Kuusipalo 1985). Frey (1973) has underlined that in extreme conditions the boundaries between site types are usually well-marked; though the greater the number of species, the smaller the role of dominant species, and as soon as one considers mesic conditions, the task to separate the sites according to their type turns out to be rather complicated.

In the current study our attempt is to testify (i) how uniform the soil conditions within the limits of one Estonian mesic forest site type communities are, i.e. whether they represent 'biologically equivalent' habitats *sensu* Cajander (1926, 1930) having approximately equal growth rate/productivity of trees, (ii) how similar the species content of the same forest site type communities in different districts of Estonia is, (iii) how the species content similarity/discrepancy is expressed in different layers of forest communities and, (iv) which environmental factors determine the species richness and composition in the considered communities most essentially.

Materials and methods

We took under study the mesic *Hepatica* site type forests having an intermediate ecological position between the eutrophic but comparatively dry calcareous *Calamagrostis* site type forests ('loo' [lô:] forests, in Estonian), mesotrophic mesic *Oxalis* site type forests and eutrophic fresh *Aegopodium* site type forests. Thus, the *Hepatica* site type forests grow in habitats characterized with mesic moisture conditions and good trophicity. These stands can be found on undulating tilly plains, drumlins, eskers and low hillocks in the central as well as in the northern and north-western parts of Estonia on deeper Rendzic Leptosols, Calcaric Regosols, Calcaric and Mollic Cambisols and Calcaric Luvisols, which have been formed on calcareous yellowish-grey till. The latter soils occur also in southern Estonia on reddish-brown till parent material and are potentially highly productive (Lõhmus 1974a,b, Paal 1997).

The total area of *Hepatica* site type forests in Estonia is 210700 ha or 9.5% of the forest land (Pärt et al. 2009). Spruce forests are the most common (57%), while pine (27%) and birch stands (10%) are the next in importance; forests dominated by aspen, grey alder or oak occur sparsely. The stands belong to the quality classes Ia to II (III) but often the potentially high productivity of these habitats is not realized by the tree stand. This is caused by the damages of the fungus causing butt rot and by the attacks of bark beetles and premature rarefaction of stands which accompany these damages (Karoles 1995).

Sample areas

The fieldwork was carried out in Rapla district (Raplamaa) in northwestern Estonia, in the Otepää Nature Park, and in the Karula National Park situated both in southern Estonia (Fig. 1).

Topographically Raplamaa is a part of the Harju Plateau where the landscape is dominated by limestone plains, locally also by tilly plains. The Otepää Nature Park and the Karula National Park are confined to the Otepää and Karula uplands, respectively. The Otepää Upland has evolved during ice ages on bedrock upland made of sandstones, while the Karula Upland has

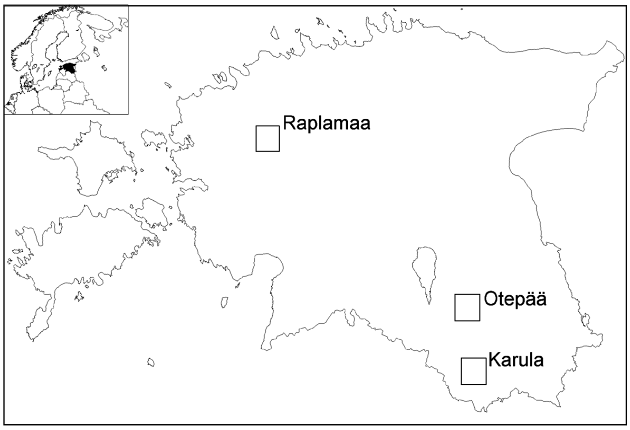

Figure 1. Location of study areas

formed as an edge formation between continental glaciers in the late glacial period on the same sandstone basement (Arold 2005).

Data sampling

In the studied *Hepatica* site type forests, *Pinus sylvestris* prevails in the first tree sublayer, while in the second sublayer *Picea abies* can be abundant. Forests in the sample were represented with (i) intensively managed stands and, (ii) modestly managed subnatural stands. Management intensity was estimated according to the information about regular cuttings as the typical management of Estonian forests presumes thinnings at 20-year intervals (Kaar 1986). Therefore, if the planned intermediate cuttings were not done, the stand was qualified as subnatural; if these cuttings were all done in time, i.e. there were stumps and openings of thinnings in the forests; the stand was interpreted as intensively managed. Stands without regular intermediate cuttings but with some cuttings because of windstorm impairment in 1967, were also included in subnatural stands. Forests of every management class were further divided into two groups: (i) younger forests about 40-80 years of age and (ii) forests older than 120 years. All in all, 37 stands were included in the sample: 12 at Raplamaa, 15 in the Otepää Nature Park and 10 in the Karula National Park.

For data collection a circular sample plot with a radius of 25 metres (ca 0.2 ha) was analyzed in each stand. If necessary, for remaining within the same community, the shape of sample plots was changed a little, maintaining the same surface area.

The tree layer was described by tree-trunks basal area, which was measured for every tree species at breast height (DBH) in every sample plot 4-5 times, average values being used for further analysis. The bush layer was described by counting the number of stems of all species on five randomly placed subplots with a radius of 2 m. The average height of stems was also estimated. The value of average stem height multiplied with the number of stems was used for analyses. Trees lower than 5 m and/or with a breast height diameter less than 5 cm were considered belonging to the bush layer. Cover percentage of every ground vegetation species was estimated on 12 randomly placed 1x1 m quadrates, species growing on sample plot but not registered on quadrates were also included into the data for species richness analysis.

For the morphological description of the soils, a pit was dug in the middle of sample plots. In every pit the deepness of occurrence of free carbonates was detected by 10% HCl. In the laboratory the following soil properties of the humus horizon and of the horizon under that were estimated: (i) pH_{H2O}, (ii) pH_{KCl}, (iii) percentage of the organic C content by oxidation of all organic matter with $K_2Cr_2O_7$ (Воробьева 1998); from this also the percentage of the humus content was calculated, (iv) percentage of total nitrogen by the Kjeldahl method (van Reeuwijk 1995), (v) soil specific surface area (m^2g^{-1}) by the water steam adsorption method (Klute 1986). All analyses were performed from the fine soil fraction with a diameter less than 2 mm. Soils were classified according to the morphological characteristics and texture class of the diagnostic horizons; if necessary, the properties estimated in the laboratory were taken into account.

The names of vascular plant species are given by Leht (2007) and the nomenclature of bryophytes by Ingerpuu and Vellak (1998). Nomenclature of soil types refers to the WRB (2006).

Data processing

Correlation structure, variation of soil properties and estimation of shared variation between soil properties and categorical variables ‘Age’ and ‘Management’ were analysed by the Partial Principal Component Analysis (Ter Braak and Šmilauer 2002) where the categorical factors were treated as covariables. The General Linear Model Analysis (GLM) was used to evaluate the difference between the environmental variables of three study areas and of forests of different age and management categories. Ecological indicator values of habitat lightness, soil moisture and nitrogen content were calculated by means of calibration (Jongman et al. 1995), using the weighted averaging algorithm and indicator values of herb (Ellenberg 1979) and moss layer (Düll 1991) plant species.

To test which environmental variables affect the forest ground vegetation species richness, the GLM analysis was applied (StatSoft 2001).

For ordination of vegetation data, first the length of the species and environmental variables variation gradient was estimated by the Detrended Correspondence Analysis (DCA). If the gradient length appeared to be relatively short (<2 SD), subsequently the Principal Components Analysis (PCA) was used; if the gradient length was longer (>2 SD), the Detrended Correspondence Analysis (DCA) was exploited (Ter Braak and Šmilauer 2002). Detrending was done by second order polynomials. The bush, herb and moss layer data were square-root transformed and in the case of herb layer downweighting of rare species was applied. Species found only from one quadrate with cover <0.5% were removed from the moss layer species analysis.

For ranking of environmental variables according to their importance for determining the species data variation structure, the forward selection procedure available in the Redundancy Analysis (RDA) in case of short gradient and the Canonical Correspondence Analysis (CCA) in case of longer gradient was used. The significance of variables was evaluated by the Monte Carlo permutation test (1000 permutations). Variables 'Age' and 'Management' interaction was removed from the analysis due to the high value (>20) of the variance inflation factor, indicating multi-collinearity with some other environmental variables (Ter Braak and Šmilauer 2002).

The Multi-Response Permutation Procedure (MRPP; McCune and Mefford 1999) was carried out to test species composition differences between the forests of three study areas, as well as between their age and management classes.

The classificatory indicator values of species in the considered study areas were calculated by the Dufrêne and Legrendre (1997) method included into the program package PC-ORD (McCune and Mefford 1999). Herb and moss layer species found only in one quadrat with cover <0.5% were removed from this analysis. The statistical significance of the obtained indicator values was evaluated by the Monte Carlo permutation test.

Relationship between the forest's age and their site index H100, referring to the dominant height (in metres) of the tree stand of a reference age of 100 years (Lahti 1995) was calculated by regression analysis. Site index H100 has been considered as a reliable indicator of site fertility (Kuusipalo 1985). For that analysis an independent sample of 800 stands for Raplamaa, 238 and 157 stands for the Otepää and Karula Uplands was used. All these data were taken from the Estonian State Forest Inventory Database. The significance of differences between the H100 indices, timber volume, trees height and diameter in three study areas were tested by the One-Way ANOVA. Pairwise multiple comparisons were performed by Tukey's HSD test (StatSoft 2001).

Results

Environmental conditions

The soils of the investigated areas differ rather remarkably by their morphology as well as by their chemical properties. For soils of Karula and Otepää sample areas the internal variability of soil properties is also rather large, whereas the soils of Raplamaa are more congeneric.

The soils at Raplamaa are represented mainly by Rendzinas lying on bedrock limestone or having carbonate rich parent material in limestone rubble till and these soils are classified mainly as Calcaric Regosols or Calcaric Cambisols. They are characterized by the presence of rock fragments in soil profile, including limestone rubble, pebble and gravel. The abundance of coarse fragments in humus layer is staying between few and common, increasing remarkably in deeper horizons.

The thickness of humus horizon in the studied profiles of Raplamaa soils varies between 13 and 50 cm, being 25 cm on average (Table 1). Some investigated soils have developed a complex horizon (humus transient horizon AB) having features of humus accumulation (mostly in root channels) and illuviation processes. Most of the soils have also metamorphic illuviation of B horizon (often as the transitional horizon to the parent material). On four sample plots (Os1, Ys7, Ys8, Ym11) shallow (up to some cm) forest floor layer has been accumulated. The organic layers of those soils are usually thin, containing leaf-needle-branch litter at different decomposition stage, followed by fresh calcic mull or forest mull humus profile.

The soil properties also depend on the deepness of solum, in some cases (Ym12 and Ys7) the deepness of soil profile does not reach more than 40 cm, followed by continuous bedrock (limestone). By texture these soils are sandy loam, only one site (Ym10) is loam. The content of organic carbon varies considerably (from 0.7% in sample plot Ys9 up to 6.0% in Os2). The C:N ratio ranges between 6.2 and 23.1, the biggest C:N ratio is characteristic of the soil without forest floor layer. Soil pH_{KCl} in humus horizon is mostly below 6.5, but in deeper horizons it is increasing to the neutral (Table 1).

In the Otepää Upland, the soils of *Hepatica* site type forests have high horizontal variability, mainly due to different types of parent material and changeable topography. On carbonate rich red-brown till Rendzinas represented by Calcaric Regosols and Calcaric Cambisols have developed. On acid coarse fluvioglacial deposits where the podzolization process is going on but the spodic horizon has not emerged yet, Dystric Arenosols and Umbri-Entic Podzols can occur.

Table 1. Mean soil properties and habitats' ecological indicator values in the forests of three study areas. Notations: X – arithmetical mean, SD – standard deviation; 1 – the humus horizon, 2 – the following horizon, depth – humus horizon depth, pH_{KCl} and pH_{H2O} – soil pH in KCl and water solution; Humus and C – humus and carbon content, respectively, SSA – soil specific surface area

	Sample area					
	Raplamaa		Otepää		Karula	
Property	X	SD	X	SD	X	SD
1-depth (cm)	25.2	6.0	14.5	7.2	14.4	4.1
$1pH_{KCl}$	6.2	0.4	4.5	1.1	4.5	0.9
$1pH_{H20}$	6.5	0.4	4.9	1.2	5.1	1.0
1Humus (%)	4.3	2.3	2.7	0.7	4.2	1.7
1C (%)	2.5	1.3	1.6	0.4	2.4	1.0
1SSA (m^2g^{-1})	69.7	15.1	42.5	9.5	45.5	17.4
$2pH_{KCl}$	6.7	0.5	5.0	1.3	4.7	1.2
$2pH_{H20}$	7.0	0.5	5.4	1.4	5.2	1.3
2Humus (%)	1.5	1.0	0.8	0.4	1.1	0.5
2C (%)	0.9	0.6	0.4	0.2	0.6	0.3
2SSA (m^2g^{-1})	42.9	15.8	25.3	7.9	22.6	8.5
Habitats' ecological indicator values						
Nitrogen	5.1	0.6	5.2	0.4	5.0	0.5
Lightness	5.3	0.5	4.9	0.7	4.8	0.6
Moisture	4.5	0.2	4.7	0.1	4.9	0.2

The third group includes soils which are relatively acid in upper horizons where pH_{KCl} is between 2.9 and 4.9 but in deeper horizons and/or in parent material the pH_{KCl} increases over 7.0. These soils belong to Endoeutric Arenosols. The decomposing conditions for litter were usually good and therefore only 1-3 cm thick litter layer was detected. The thickness of A-horizon varies in limits of 8 to 24 cm, having the mean value of 14.5 cm.

In the Karula Upland, Calcaric Regosols and Calcaric Cambisols have developed on calcareous rich parent material, while Endoeutric Arenosols have some free carbonates in the lower part of profile. On acid sands Dystric Arenosols as well as Gleyic Podzols are characteristic. Here also Stagnic Luvisols can be found in sites where the parent material with coarser texture lies on material having heavier texture. In the Karula area, soils humus horizon average thickness (14.4 cm) is the same as in the Otepää soils (Table 1). The organic carbon content is in the limits of 1.92-3.74% which is rather high considering that these soils often have acid reaction (pH_{KCl} is varying from 3.0 till 6.2). The content of organic carbon is relatively high (mean value 0.6%) also in the deeper layers below the humus horizon. In the Karula Upland and also in the Otepää Upland, the sample plots were often situated on quite deep slopes where in some cases the vegetation was considerably sparse and the soil surface subjected to the degradation due to erosion. That leads to the shallower humus horizon and the lower content of organic carbon in the humus horizon, whereas in the lower parts of hillocks the evidence of soil accumulation was recorded.

On the environmental variables ordination plot obtained by the partial PCA the soils of the Otepää stands are situated on the left side, while the soils of the Karula forests have an intermediate position along the first axis (Fig. 2). Variation along that axis is determined mainly by the soil properties such as humus horizon specific surface area, pH and humus content. With the second ordination axis humus horizon depth and habitat moisture have the strongest correlation. The calcareous soils (Calcaric Cambisols and Calcaric Regosols) of the Raplamaa forests are rather obviously located on the right side of the ordination plot, in the first and second quarter. It asserts that these soils have

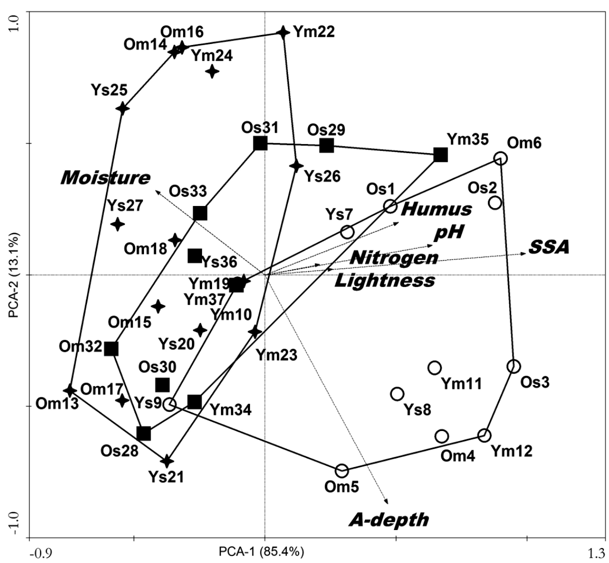

Figure 2. Ordination of soil data according to the Partial Principal Component Analysis. Variables 'Age' and 'Management' were treated as covariables. Notations: pH – pH of soil humus horizon in KCl solution, SSA – soil humus horizon specific surface area (m^2g^{-1}), A-depth – depth of soil humus horizon (cm), Humus – content of humus (%) in humus horizon; Nitrogen, Lightness and Moisture – respective indicator values of habitats'. Forests of Raplama district are indicated with circles, forests of Otepää Nature Park with daimonds and forests in Karula National Park with squares. Os – old sub-natural forest, Om – old intensively managed forest, Ys – young sub-natural forest, Ym – young intensively managed forest

the highest value of properties positively correlated with the first ordination axis. The moisture gradient is directed from the second to the fourth quarter, i.e. the Raplamaa forests are usually drier than forests at Karula or Otepää. Considered environmental variables have very little (<1%) shared variance with variables 'Age' and 'Management'.

According to the GLM analyses (Table 2) pH, soil specific surface area, humus horizon depth and moisture differ significantly between the study areas but that result follows from the clear difference of Raplamaa forests soils, while in the Otepää and Karula stands several soil properties are rather similar (Fig. 3). The variable 'Management' does not affect the environmental parameters significantly, whereas variable 'Age' has important effect for habitats light conditions (Table 2). The habitat lightness index is greater in younger forests than in older stands. Variables 'Age' and 'Management' interaction appeared to be important for humus horizon pH, specific surface area and the nitrogen content. In the younger forests latter parameters are higher in intensively managed forests than in subnatural stands but this difference is significant only in the case of pH (Fig. 4).

Species richness

In total, 221 vascular plant and 79 bryophyte species were recorded in the studied forests. Among them 24 vascular plant and 8 bryophyte species occurred with the frequency of more than 75%, e.g. *Rubus idaeus* (100%), *R. saxatilis* (100%), *Sorbus aucuparia* (100%), *Luzula pilosa* (97%), *Oxalis acetosella* (97%),

Table 2. Effect of categorical variables ‚Area', ‚Management' and ‚Age' on soil properties and habitats' ecological indicator values according to the General Linear Model analyses. Notations: Area – sample area, M – management class, Age – age class, other notations as in Table 1. In Table the values of F-criterion are presented, with stars the significance levels are marked: *p <0.05, **p <0.001

Dependent variable	Variable				Intercept
	Area	M	Age	M x Age	
Soil properties					
pH_{KCl}	18.7**	3.7	0.7	5.0*	1407.1**
Humus (%)	2.8	0.1	2.4	0.6	231.9**
SSA (m^2g^{-1})	17.3**	0.4	0.1	5.8*	685.1**
A-depth (cm)	11.0**	0.1	0.4	0.1	175.5**
Habitats' ecological indicator values					
Nitrogen	2.2	<0.1	2.1	7.1*	4334.6**
Lightness	2.3	0.2	4.8*	0.1	2473.9**
Moisture	21.1**	0.2	0.4	<0.1	35915.5**

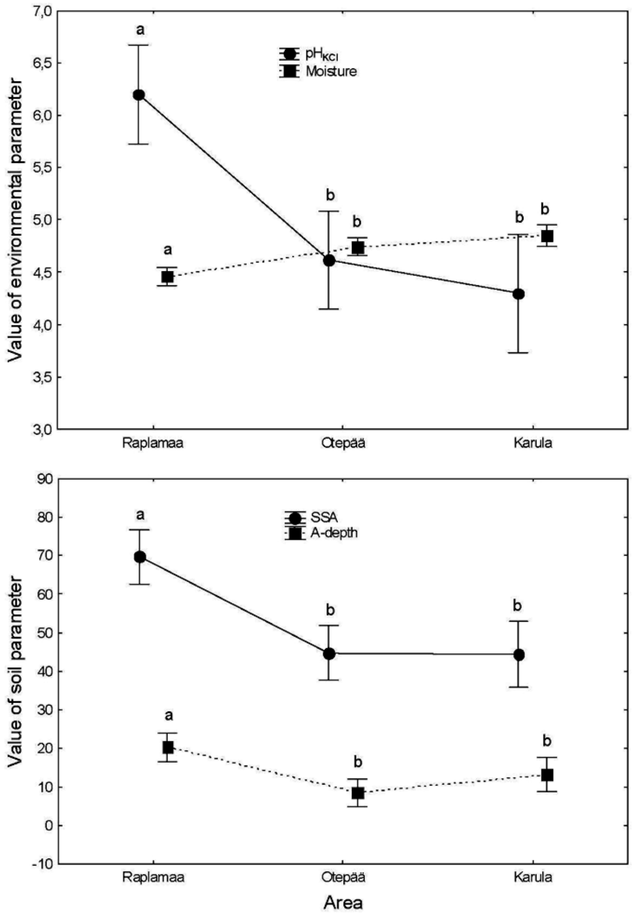

Figure 3. Average value of environmental variables in study areas. Notations: pH_{KCl} – pH of soil humus horizon in KCl solution, Moisture – habitats' moistue calculated by species ecological indicator values, SSA – soil humus horizon specific surface area (m^2g^{-1}), A-depth – soil humus horizon depth (cm). Letters a and b refer differences between groups by the Tukey's HSD test

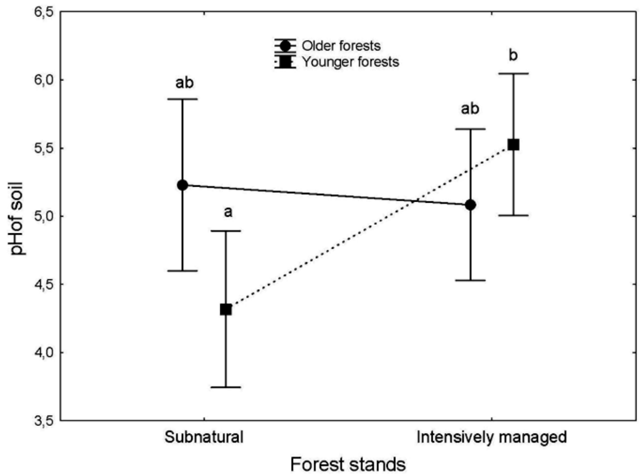

Figure 4. Average pH value of soil humus horizon in forests of different age and management categories (variables ‚Age' and ‚Management' interaction). Notations as in Figure 3

Cirriphyllum piliferum (97%), *Fragaria vesca* (95%), *Maianthemum bifolium* (92%), *Hylocomium splendens* (92%), *Solidago virgaurea* (89%), *Plagiomnium affine* (89%), *Rhytidiadelphus triquetrus* (89%) etc.

The average species richness of vascular plants per stand was 68 in Raplamaa, 61 at Otepää and 57 at Karula. The corresponding numbers for moss layer were respectively 22, 18 and 18. Differences between these values in the forests of three study areas are not statistically reliable.

The vascular plant species richness was the highest in a Raplamaa sub-natural younger stand (Ys7) – 87 species, and lowest in an Otepää intensively managed older stand (Om13) – 35 species. The moss layer species richness was also the highest in a Raplamaa sub-natural younger stand (Ys9) – 37 species, and the lowest in an Otepää intensively managed younger stand (Ym22) – 9 species.

The GLM analysis proves that the diversity of herb layer species is significantly affected only by the habitat lightness (Table 3). Increase in habitat lightness enhances the number of vascular plant species (Fig. 5). We did not discover any analysed environmental variable, which had a significant effect on the species richness of the moss layer.

Moss layer

The MRPP test proves that the moss layer species composition in the Raplamaa stands differs significantly (p < 0.001) from that in the respective forests of the Otepää and Karula uplands, while forests of both southern Estonian study areas have similar species content (p = 0.112). Ordination of bryophyte

Table 3. Effect of the environmental factors on the diversity of vascular plant species by the General Linear Model analysis. Notations: F – value of the F-criterion, p – significance level, Slope – slope of the regression line, SE – its standard error, MossCov – total coverage of moss layer. Other notations as in Tables 1 and 2

Factor	F	p	Slope	SE
Intercept	1.0	0.318		
Area	0.3	0.771		
M	<0.1	0.833		
Age	0.8	0.383		
M*Age	0.3	0.596		
pH_{KCl}	0.6	0.442	1.976	2.524
Humus (%)	0.6	0.433	1.108	1.389
SSA (m^2g^{-1})	<0.1	0.906	0.022	0.183
A-depth	0.2	0.662	0.148	0.334
Nitrogen	0.1	0.781	-1.605	5.699
Lightness	4.7	0.040	9.311	4.285
Moisture	1.9	0.187	17.134	12.588
MossCov	2.9	0.104	0.143	0.084

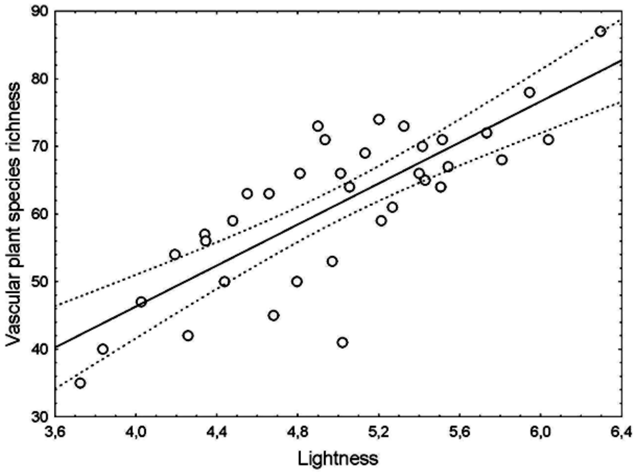

Figure 5. Relationship between the number of vascular plant species and habitat's lightness indicator value

data (Fig. 6) illustrates these results explicitly – Raplamaa stands are obviously separated from others but the Otepää and Karula forests occupy almost the same area on the ordination plot. Several calcifilous species (Düll 1991), such as *Brachythecium populeum*, *Fissidens bryoides*, *F. taxifolius* and *Homalothecium lutescens* were recorded only in the Raplamaa forests (Table 4). *Plagiochila asplenioides*, *P. porelloides, Plagiomnium affine* and *Rhodobryum roseum* are significant indicator species for Otepää area, whereas *Atrichum undulatum, Brachythecium rutabulum* and *Eurhynchium hians* are mostly confined to the Karula *Hepatica* site type forests.

It is difficult to see any clear regularity on the ordination scheme in the location of sample plots according to the stands age or management intensity. Still, more old stands are situated in the third quarter. According to the MRPP tests the species composition in forests of different age and management categories do not differ either.

The moss layer species variance is described significantly (p < 0.05) by the variables 'Area' (20%), herb layer cover (15%), bush layer species total abundance (7%), humus horizon pH (6%), habitat lightness (5%), DBH of deciduous trees (4%) and humus horizon depth (3%). These variables explain all in all 60% of the moss layer species composition, while the whole model refers 69% of the species variance (Table 5).

Herb layer

In the DCA ordination plot of herb layer data the stands of different study areas are distinctly separated from each other (Fig. 7). The species composition of these three areas is also different (p <0.001) by the MRPP test. Difference is less expressed and not significant (p = 0.092) by pairwise comparison of the Ra-

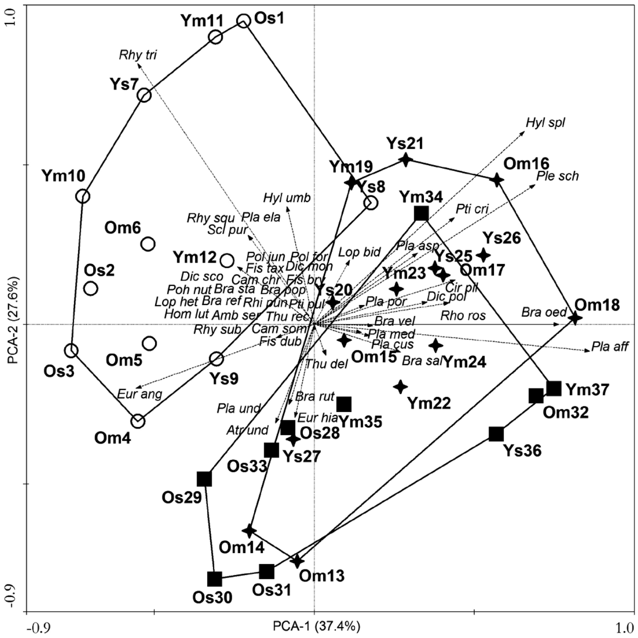

Figure 6. Ordination of moss layer data by the Principal Component Analysis. Abbreviations of species names: *Amb hum – Amblystegium humile, Amb ser – Amblystegium serpens, Amb sub – Amblystegium subtile, Amb var – Amblystegium varium, Ble tri – Blepharostoma trichophyllum, Bra oed – Brachythecium oedipodium, Bra ref – Brachythecium reflexum, Bra sal – Brachythecium salebrosum, Bra sta – Brachythecium starkei, Bra vel – Brachythecium velutinum, Cam chr – Campylium chrysophyllum, Cam som – Campylium sommerfeltii, Cep rub – Cephaloziella rubella, Cir pil – Cirriphyllum piliferum, Dic mon – Dicranum montanum, Dic pol – Dicranum polysetum, Fis bry – Fissidens bryoides, Her sel – Herzogiella seligeri, Hyl spl – Hylocomium splendens, Hyl umb – Hylocomium umbratum, Hyp cup – Hypnum cupressiforme, Hyp pal – Hypnum pallescens, Lop bid – Lophocolea bidentata, Lop het – Lophocolea heterophylla, Now cur – Nowellia curvifolia, Pla cur – Plagiothecium curvifolium, Pla cus – Plagiomnium cuspidatum, Pla den – Plagiothecium denticulatum, Pla ela – Plagiomnium elatum, Pla lae – Plagiothecium laetum, Pla med – Plagiomnium medium, Pla nem – Plagiothecium nemorale, Pla rut – Plagiothecium ruthei, Pla und – Plagiomnium undulatum, Ple sch – Pleurozium schreberi, Poh nut – Pohlia nutans, Pol for – Polytrichum formosum, Pol jun – Polytrichum juniperinum, Pti cri – Ptilium crista–castrensis, Pti pul – Ptilidium pulcherrimum, Rad com – Radula complanata, Rhi pun – Rhizomnium punctatum, Rhy squ – Rhytidiadelphus squarrosus, Rhy sub – Rhytidiadelphus subpinnatus, San unc – Sanionia uncinata, Thu del – Thuidium delicatulum, Thu rec – Thuidium recognitum.* Other notations as in Figure 2

plamaa and Otepää data. The list of significant indicator species for every study area is quite long (Table 6). Some indicator species of the Raplamaa forests were recorded only there: *Carex ornithopoda* (frequency 83%), *Carex flacca* (67%), *Rubus caesius* (58%) and

Table 4. Relative frequency of moss layer indicator species in different study areas. Notations: R – Raplamaa, O – Otepää, K – Karula, p – significance level

Species	Relative frequency			Area	p
	R	O	K		
Brachythecium populeum	25	0	0	R	0.041
Dicranum scoparium	75	60	30	R	0.020
Eurynchium angustirete	92	33	70	R	0.036
Fissidens bryoides	17	0	0	R	0.173
Fissidens dubius	42	7	10	R	0.020
Fissidens taxifolius	33	0	0	R	0.013
Herzogiella seligeri	58	7	30	R	0.017
Homalothecium lutescens	25	0	0	R	0.047
Hypnum cupressiforme	58	13	20	R	0.026
Lophocolea heterophylla	100	80	80	R	<0.001
Nowellia curvifolia	25	0	0	R	0.044
Rhytidiadelphus triquetrus	100	93	70	R	<0.001
Sanionia uncinata	83	60	20	R	0.011
Scleropodium purum	42	0	0	R	0.001
Plagiomnium affine	75	100	90	O	0.048
Plagiochila asplenioides	58	67	20	O	0.044
Plagiochila porelloides	8	33	0	O	0.040
Rhodobryum roseum	50	100	60	O	0.001
Atrichum undulatum	17	7	40	K	0.049
Brachythecium rutabulum	8	47	90	K	0.027
Eurynchium hians	25	0	40	K	0.024

Table 5. The environmental variables having significant effect on variance of different layers of vegetation; variance decomposition is based on the CCA (in case of herb layer) or RDA space. Notations: λ_1 – coefficient describing the variable own variance, λ_A – coefficient characterizing the additional variance what each variable explains at its time of inclusion in the model, HerbL – total cover of herb layer, BushL – value of bush stems average height multiplied with the number of stems, TreeLDec – basal area of deciduous trees. Other notations as in Table 1 and 3

Variable	λ_1	λ_A	F	p
		Moss layer		
Area	0.20	0.20	8.70	0.001
HerbL	0.15	0.15	7.89	0.001
BushL	0.11	0.07	4.06	0.004
pH_{KCl}	0.15	0.06	3.57	0.001
Lightness	0.13	0.05	3.24	0.004
TreeLDec	0.08	0.04	3.01	0.008
A-depth	0.10	0.03	2.13	0.036
		Herb layer		
Area	0.24	0.24	3.75	0.001
Nitrogen	0.16	0.16	2.76	0.001
A-depth	0.11	0.10	1.73	0.013
Lightness	0.16	0.10	1.66	0.015
pH_{KCl}	0.13	0.09	1.50	0.041
		Bush layer		
Area	0.15	0.15	6.40	0.001
Lightness	0.07	0.14	6.56	0.001
Age	0.11	0.09	4.51	0.001
A-depth	0.11	0.04	2.15	0.050
		Tree layer		
Area	0.19	0.19	7.95	0.002
SSA	0.06	0.06	3.08	0.044

Filipendula vulgaris (50%). *Moehringia trinervia* has a high indicator value for the Otepää forests and occurred there with the frequency of 75%. Grouping forests by their age and management categories, the difference of herb layer species composition appears to be insignificant.

The partial CCA forward selection procedure proves that the variables significantly explaining the herb layer species variance are 'Area' (10%), followed by indicator values of nitrogen (7%) and lightness (4%), humus horizon depth (4%) and pH_{KCl} (4%) (Table 5). These variables explain together 28% of the herb layer species composition, while the whole model describes 49% of the species variance.

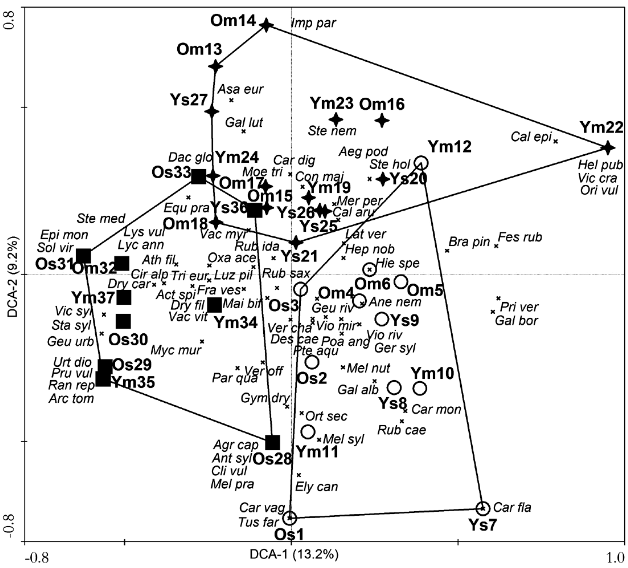

Figure 7. Ordination of herb layer data by the Detrended Correspondence Analysis. Abbreviations of species names: *Act spi – Actaea spicata, Agr cap – Agrostis capillaris, Ant syl – Anthriscus sylvestris, Arc tom – Arctium tomentosum, Asa eur – Asarum europaeum, Ath fil – Athyrium filix–femina, Bra pin – Brachypodium pinnatum, Cal epi – Calamagrostis epigeios, Cir alp – Circaea alpina, Cli vul – Clinopodium vulgare, Dac glo – Dactylis glomerata, Dry fil – Dryopteris filix–mas, Fes rub – Festuca rubra, Gal alb – Galium album, Gal bor – Galium boreale, Gal lut – Galeobdolon luteum, Gym dry – Gymnocarpium dryopteris, Hel pub – Helictotrichon pubescens, Hie spe – Hieracium* sp.*, Imp par – Impatiens parviflora, Lyc ann – Lycopodium annotinum, Lys vul – Lysimachia vulgaris, Mai bif – Maianthemum bifolium, Mel nut – Melica nutans, Mel pra – Melampyrum pratense, Mel syl – Melampyrum sylvaticum, Mer per – Mercurialis perennis, Ori vul – Origanum vulgare, Poa ang – Poa angustifolia, Pri ver – Primula veris, Pru vul – Prunella vulgaris, Pte aqu – Pteridium aquilinum, Ran rep – Ranunculus repens, Rub ida – Rubus idaeus, Ste hol – Stellaria holostea, Ste nem – Stellaria nemorum, Tus far – Tussilago farfara, Vac myr – Vaccinium myrtillus, Vac vit – Vaccinium vitis–idaea, Ver cha – Veronica chamaedrys, Ver off – Veronica officinalis, Vic cra – Vicia cracca, Vic syl – Vicia sylvatica.* Other notations as in Figure 2

Table 6. Relative frequency of herb layer indicator species in different study areas. Notations as in Table 4

Species	Relative frequency			Area	p
	R	O	K		
Anemone nemorosa	92	73	20	R	0.001
Aquilegia vulgaris	75	0	0	R	<0.001
Carex flacca	50	0	0	R	0.001
Carex montana	75	0	0	R	<0.001
Carex ornithopoda	83	0	0	R	<0.001
Carex vaginata	58	0	0	R	<0.001
Elymus caninus	50	13	10	R	0.018
Filipendula vulgaris	42	0	0	R	0.001
Fragaria vesca	100	87	100	R	<0.001
Geranium sylvaticum	100	27	0	R	<0.001
Geum rivale	58	20	10	R	0.024
Hepatica nobilis	100	87	20	R	0.003
Hieracium spendens	58	0	0	R	0.001
Lathyrus vernus	75	53	0	R	0.037
Luzula pilosa	100	93	90	R	0.031
Orthilia secunda	83	20	20	R	0.014
Paris quadrifolia	100	40	50	R	0.001
Ranunculus bulbosus	67	13	10	R	0.001
Rubus caesius	67	0	0	R	<0.001
Rubus saxatilis	100	100	100	R	0.004
Taraxacum officinale	100	80	40	R	0.035
Valeriana officinalis	33	0	0	R	0.011
Viola mirabilis	100	67	10	R	0.001
Viola riviniana	100	47	70	R	<0.001
Aegopodium podagraria	33	73	0	O	<0.001
Calamagrostis arundinacea	67	93	20	O	<0.001
Carex digitata	33	93	60	O	0.012
Convallaria majalis	25	60	20	O	0.023
Moehringia trinervia	0	40	0	O	0.004
Dryopteris carthusiana	0	60	90	K	<0.001
Epilobium montanum	0	7	40	K	0.006
Equisetum pratense	0	33	50	K	0.034
Geum urbanum	8	0	70	K	<0.001
Mycelis muralis	83	53	100	K	<0.001
Solidago virgaurea	33	33	90	K	<0.001
Stachys sylvatica	0	0	30	K	0.015
Stellaria media	0	7	100	K	<0.001
Trientalis europea	8	47	60	K	0.009
Urtica dioica	0	7	50	K	0.003

Bush layer

The stands of different study areas are separated rather clearly also according to the PCA ordination of bush layer data (Fig. 8). Most of the Raplamaa forests are positively correlated with the first axis; the majority of Otepää forests have positive and the majority of the Karula forests negative correlation with the second axis. Species such as *Corylus avellana, Padus avium* and *Rhamnus catharcticus* are statistically relevant ($p < 0.05$) indicator species of the Raplamaa forests' bush layer. *Lonicera xylosteum* and *Ribes alpinum* appear to be bush layer indicator species ($p < 0.05$) for the Otepää forests, and *Alnus incana* for the Karula stands. The MRPP test confirms that bush layer species composition in the Raplamaa forests is significantly different from that at Otepää (p=0.017) and Karula (p=0.016), whereas bush layer in forests of southern Estonian study areas is similar (p = 0.235).

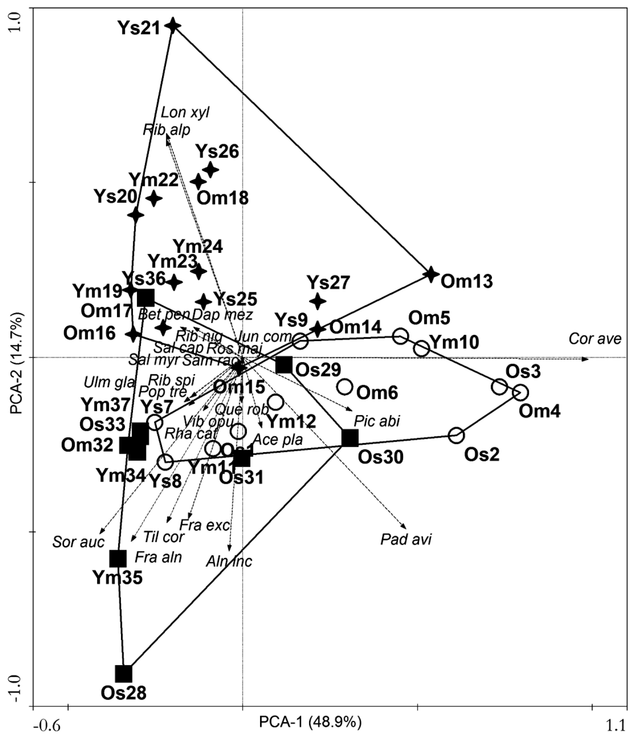

Figure 8. Ordination of bush layer data by the Principal Component Analysis. Abbreviations of species names: *Ace pla – Acer platanoides, Aln inc – Alnus incana, Bet pen – Betula pendula, Cor ave – Corylus avellana, Dap mez – Daphne mezereum, Fra aln – Frangula alnus, Fra exc – Fraxinus excelsior, Jun com – Juniperus communis, Lon xyl – Lonicera xylosteum, Pad avi – Padus avium, Pic abi – Picea abies, Pop tre – Populus tremula, Que rob – Quercus robur, Rha cat – Rhamnus catharcticus, Rib alp – Ribes alpinum, Rub cae – Rubus caesius, Rib nig – Ribes nigrum, Rib spi – Ribes spicatum, Rub ida – Rubus idaeus, Sor auc – Sorbus aucuparia, Til cor – Tilia cordata, Ulm gla – Ulmus glabra, Vib opu – Viburnum opulus, Sal cap – Salix caprea, Sal myr – Salix myrsinifolia, Sam rac – Sambucus racemosa, Ros maj – Rosa majalis.* Other notations as in Figure 2

Bush layer species composition is different in older and younger stands. *Corylus avellana* has significant ($p < 0.05$) indicator value for older stands.

The variables significantly explaining the bush layer species variance are 'Area' (15%), habitat lightness (14%), stand age (9%) and humus horizon depth (4%) (Table 5). All together these variables explain 42% of the bush layer species variation, while the whole model explains 59% of the variance.

Tree layer

By the tree layer basal area data the stands of three study areas are rather largely overlapping on the PCA ordination plot (Fig. 9). Nevertheless, most of the Karula stands are positively, and the Raplamaa stands negatively correlated with the first axis, while the Otepää forests have overwhelmingly a positive relationship with the second axis. In the tree layer of the Karula forests pine has a dominating position, whereas in the tree layer (mainly in the second sublayer) of the Otepää stands spruce has more prominent position. According to the MRPP test, the tree layer species composition in the Raplamaa forests differs significantly from that at Otepää (p = 0.005) and Karula (p = 0.004), while forests of both southern Estonian study areas are similar to each other (p = 0.152). Within the forests of considered age and management categories the tree layer species composition does not differ by the MRPP tests substantially.

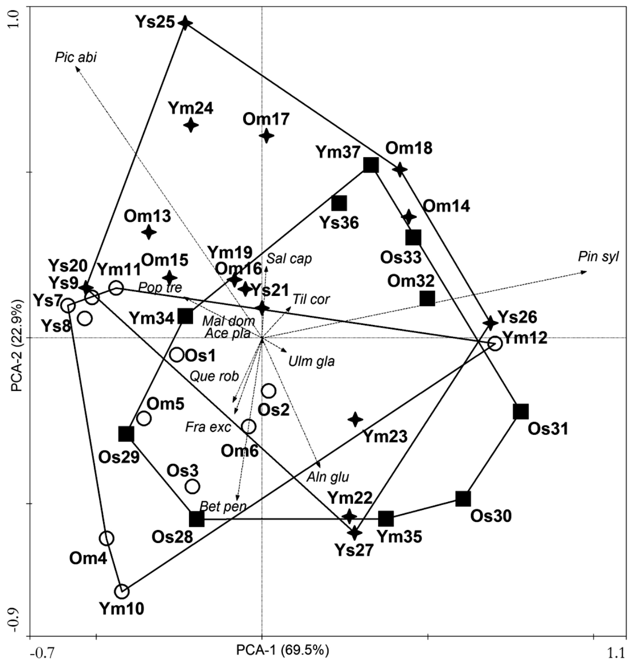

Figure 9. Ordination of tree layer data by the Principal Component Analysis. Abbreviations of species names: *Pin syl – Pinus sylvestris, Pic abi – Picea abies, Bet pen – Betula pendula, Pop tre – Populus tremula, Ace pla – Acer platanoides, Fra exc – Fraxinus excelsior, Til cor – Tilia cordata, Sal cap – Salix caprea, Ulm gla – Ulmus glabra, Que rob – Quercus robur, Aln inc – Alnus incana, Mal dom – Malus domestica.* Other notations as in Figure 2

By the partial RDA forward selection procedure, the variables significantly explaining the tree layer species variance are 'Area' (19%) and soil humus horizon special surface area (6%) (Table 5). The whole model explains 38% of the species variance.

Tree layer growth dynamics in all three regions is generally similar (Fig. 10) but in Raplamaa the average site quality class is 2.3, at Otepää and Karula 1.5. According to that also the height of trees, diameter of stems and timber volume are at Raplamaa essentially lower than in Otepää and Karula uplands (Fig. 11).

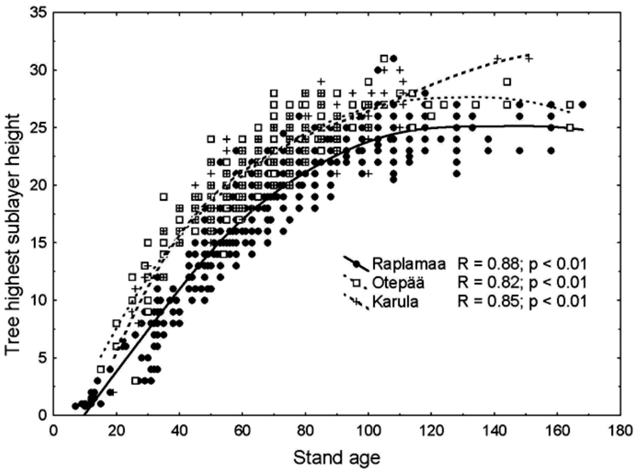

Figure 10. Relationship between the stand age and the average height of tree highest sublayer

Discussion and conclusions

We did not discover any variable with a significant effect on the bryophyte species richness among the considered variables, whereas the species richness of vascular plants had a positive feedback to the habitats lightness. Several studies of half-open wooded meadows (Kull and Zobel 1991, Austad and Losvik 1998, Linusson et al. 1998, Einarsson and Milberg 1999), calcareous *loo* forests (named earlier in some respects incorrectly as 'alvar' forests) (Meier et al. 2005) and also of old *Hepatica* and *Aegopodium* site type forests (Sepp and Liira 2009) confirm this correlation. However, species richness of different forest types is not always favoured by increasing lightness, therefore the positive relationship between species richness and habitats lightness in some forest communities is not valid for all stands (Härdtle et al. 2003).

The average species richness of vascular plants and bryophyte species in all three study areas appeared to be rather similar, nevertheless, that does not mean also species content similarity. The ordination analyses proved that the similarity/discrepancy of the species content in various layers of forest communities is expressed to a rather different extent, i.e. every layer develops and forms its structure at least to some extent autonomously. Certain independence of layers in forest plant communities also became evident on the ground that the species variance in every community layer has been determined usually with different en-

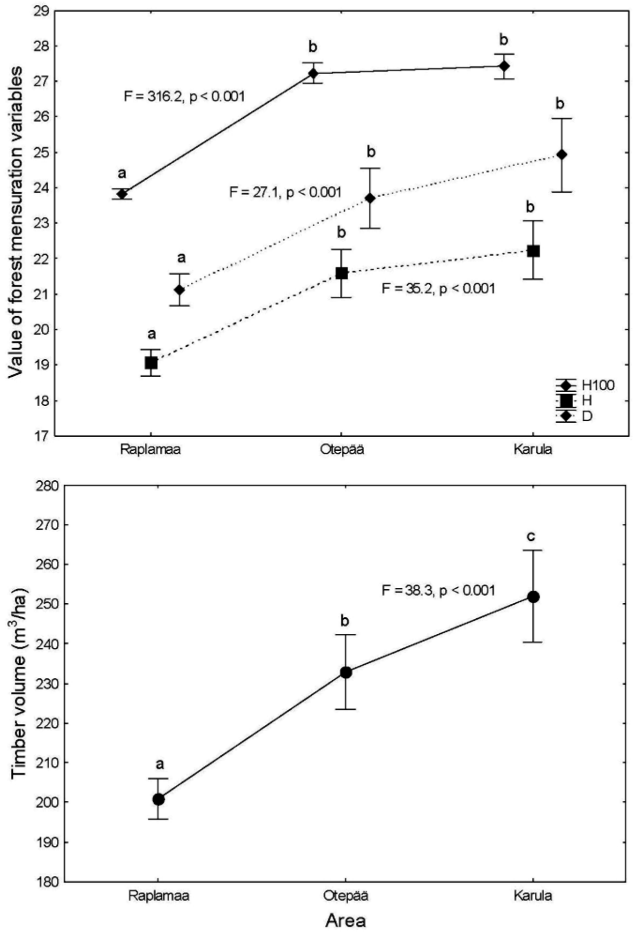

Figure 11. Differences between forest's mensuration variables in three study areas by the One-Way ANOVAs. Notations: H100 – site index referring to the dominant height of trees at age of 100 years, H – trees height (m), D – trees diameter (cm), F – value of the F-criterion, p – significance level. Letters a, b and c refer differences between groups by the Tukey's HSD test

vironmental variables, consequently, for every layer its own system of relationships between the species as well as between the species and environmental factors is characteristic (Шенников 1964, Paal 1995). The relative autonomy of plant community layers is in good accordance with Cajander's theory of forest site types (Cajander 1930, Kalela 1960, Frey 1973).

By our data the impact of neither management nor age factors on the species composition, except bush layer, was not significant. In *Hepatica* site type forests the bush layer formed mainly by hazel is common and in older stands it often constitutes a dense canopy, being the reason why stand age appeared to be an important variable for that layer. According to Sepp and Liira (2009), at least in the *Hepatica* site type old forests management affects the field layer species composition substantially. It seems that the only modest effect of management and age factors in the current study is overshadowed by the large variance connected with the categorical variable 'Area'.

As it was shown in the results, the species content in the Raplamaa *Hepatica* site type forests differs remarkably from that in South Estonian respective stands. Recently Sepp and Liira (2009) proved a considerable effect of geographic location factor on understory species composition in the same site type forests as well. Distribution limits of numerous plant species in Estonia are conditioned by soils calcareousness. For that reason several indicator species of the Raplamaa forests are spread only or mainly in western Estonia, e.g. *Scleropodium purum* (Ingerpuu et al. 1994), *Carex ornithopoda*, *Carex flacca*, *Rubus caesius* and *Filipendula vulgaris* (Kukk and Kull 2005). In the Otepää Nature Park and even more in the Karula National Park the studied forests often grow on a hilly landscape as fragmented patches surrounded by cultivated arable lands; that is why in these stands besides many real indicator species several apophytic species (Kukk 1999) such as *Epilobium montanum*, *Geum urbanum*, *Stellaria media* and *Urtica dioica* were recorded. The invasion of non-forest vascular species from the neighbourhood can also be the cause of an accidental species content variation in the herb layer of some forests. Due to more abundant spruce in the tree layer of the Otepää stands, the herb layer receives less light there, and species such as *Aegopodium podagraria*, *Convallaria majalis*, *Moehringia trinervia* etc. are characteristic. According to Cajander's forest site type definition, variation of the vegetation inside one type cannot exceed the limits inherent for these forests in the course of their successional development. Still, it is rather obvious that even if we exclude the effects of human impact on species composition in southern Estonian *Hepatica* site type forests, their difference from respective stands of western Estonia remains much bigger than "accidental", "ephemeral" or "temporary" in the terms of Cajander.

Cajander's forest site type approach is primarily applied for estimating the potential productivity of different sites, as well as for giving general frames for yield tables, forest inventory etc. (Lahti and Väisanen 1987, Tonteri et al. 1990, Masing 1996). By Cajander (1923) habitats of the same site type must have a similar productivity potential within probability limits. Following this idea, the forest site type in the officially used Estonian classification system has been defined as a set of forests with a similar silvicultural effect, i.e. as complex of similar natural factors influencing the vegetation (Lõhmus 1984, Karoles 1995) and in site type delimitation it has usually been taken into account that the interior variation within the limits of one site type will not exceed more than two site quality classes (Katus and Tappo 1965).

The current analysis of the *Hepatica* site type forests growing in three different areas proves their habitats essential variation even within a small country like Estonia. Respective soils at Raplamaa are notably more calcareous than in the Otepää and Karula uplands, which follow from the closeness of limestone bedrock to the surface. Differences appeared also in humus horizon depth and chemical properties: in the Raplamaa forests this horizon is usually thicker, the soil specific surface area larger and pH higher than in southern Estonia. Still, as it was ascertained already in the 1920s, various environmental factors having direct or indirect effect to vegetation can create conditions where approximately similar plant communities will grow (Сукачев 1972). Cajander (1926, 1930) regarded these convergent communities as representing biological equivalent habitats having similar productivity of tree layer. Thus, despite discovered disagreement of soil properties in the forests of western and southern Estonia that is not a sufficient argument for treating the corresponding habitats as separate forest site types and supplementary information concerning plant cover, especially the tree layer growth must be involved.

Taking into account the considered soil chemical properties and humus horizon thickness, we would expect in the Raplamaa forest's to some extent better productivity than in southern Estonia. But as it became evident from our data, the height of the trees, their H100 index, diameter, as well as timber volume are, on the contrary, lower just at Raplamaa. This fact is explicable with the low water holding capacity of Rendzinas (Karoles 1995, Reintam and Rooma 2001) on what the Raplamaa Hepatica site type forests usually grow. In draught periods there is not enough water in these soils for a successful growth of trees. This statement is affirmed by the ecological values of moisture, which are higher for the Karula and Otepää forests than at Raplamaa.

In terms of site quality classes, the differences between the study areas are only 0.8 units, i.e. comparatively small and all analysed forests could be considered, hence, as belonging to the same site type. Though, the site quality class is surely only a rough attribute for characterisation of habitats productivity and cannot be taken as sole or main criteria for discrimination of forest site types. Here we must rely on the much more objective mensurative parameters and on that basis it is quite questionable to interpret all analysed forests as belonging to only one site type.

Usually the question of how widely or narrowly the site types are to be delimited has been regarded in forestry as having only a secondary importance. However, where they are broadly defined, Cajander himself as well as his followers have taken advantage of differentiating them into subtypes and variants and/ or facies (Cajander and Ilvessalo 1921, Kujala 1961, Frey 1973, Mikola 1982). Moreover, when we analyze the forest plant communities from geobotanical or biodiversity point of view, it is quite clear that a more detailed classification system of forest communities must be elaborated (Kuusipalo 1985). On this ground, it seems relevant to divide the Estonian *Hepatica* site type forests into two subtypes: the first of them is confined to calcareous soils in western and northern Estonia, and there the habitats productivity potential for tree layer is lower in comparison with the forests of the second subtype that grow mostly in eastern and southern Estonia on soils mainly depending on the topographical location and parent material calcareousness but having a higher tree layer productivity.

Acknowledgements

We thank PhD Allan Sims for supplying the forest inventory data. The study was supported by the Estonian Science Foundation grants 2339 and 8060, target-financing project SF0180012s09 and by the Centre of Excellence FIBIR.

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Received 08 January 2010
Accepted 18 June 2010

ВЗАИМООТНОШЕНИЯ МЕЖДУ РАСТИТЕЛЬНОСТЬЮ И СРЕДОЙ В ЭСТОНСКИХ ЛЕСАХ *HEPATICA* ТИПА МЕСТОПРОИЗРАСТАНИЯ НА ФОНЕ УЧЕНИЯ А.К. КАЯНДЕРА

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Резюме

Целью данной работы была проверка: 1) насколько однообразными являются почвенные условия в пределах одного, часто встречаемого типа местопроизрастания, имеющего по экологическим условиям эстонских лесов одно из центральных положений; 2) насколько сходным является видовой состав в лесах одного и того же типа местопроизрастания в разных регионах Эстонии; 3) насколько выражено сходство видового состава в разных ярусах этих лесных сообществ; 4) какие основные факторы среды определяют видовое разнообразие и состав рассматриваемых лесов. Было исследовано 37 лесов печеночного типа местопроизрастания в трех районах: 1) 12 сообществ в западной Эстонии на карбонатных почвах, сформированных на известняковых отложениях, 2) 15 сообществ в южной Эстонии на возвышенности Отепяэ и 3) 10 сообществ в южной Эстонии на возвышенности Карула. Почвы лесов исследованных трех регионов, особенно в западной Эстонии, оказались весьма различными, как по толщине гумусового горизонта, так и по химическим свойствам. В западной Эстонии они сформировались на известняковых отложениях, а почвы лесов южной Эстонии лежат на морене. Тем не менее, это еще не является веским аргументом для утверждения, что эти леса не относятся к одному типу местопроизрастания, т.к. сочетание разных почвенных условий могут оказывать на растительность сходный эффект, вследствие которого образуются биологически эквивалентные местопроизрастания (по терминологии Каяндера) и развиваются конвергентные сообщества с примерно одинаковой структурой. Число видов мохового и травяно-кустарничкового ярусов в лесах всех трех регионов довольно сходное. На видовое разнообразие травяного яруса позитивно влияет освещенность местопроизрастаний, в то же время как на моховой ярус существенного эффекта не оказывает ни один из учитываемых факторов. Леса всех трех районов исследований достоверно различаются по видовому составу мохового, травяно-кустарничкового и кустарникового ярусов. При этом каждый ярус имеет свою собственную систему взаимоотношений между видами, а также между видовым составом и условиями местопроизрастаний. Эти факты хорошо согласуются с теорией Каяндера. Хотя, химический состав почв в западной Эстонии как-будто более благоприятный для роста древостоев по сравнению с южной Эстонией, этому препятствует порою черезмерная сухость почв; вследствие чего высота и диаметр деревьев, как и объем древесины в лесах западной Эстонии меньше. Учитывая установленные различия, правомерно разделить рассмотриваемые леса на два подтипа местопроизрастания. Леса первого подтипа растут на карбонатной материнской породе, характерной для западной и северной Эстонии и продуктивность их древесного яруса ниже по сравнению лесами второго подтипа, свойственными южной и восточной Эстонии, где почвы сформированы на моренных отложениях и где продуктивность древостоя выше.

Ключевые слова: Каяндер, классификация, ярусы, лесохозяйство, продуктивность, типы местопрозрастания, почвы, число видов, возраст древостоя, рост деревьев