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1 Introduction

1.1 Aim of the study

Nature has been subject to human influence for thousands of years. In the course of time, semi-natural ecosystems have evolved that have been stabilised by continuous, extensive human land use. Often they provide special habitats and niches for a great diversity of flora and fauna which are not found in the regional natural ecosystems (medium disturbance leading to maximum species richness). In a time of rapid changes in agricultural and landscape management, they have become refuges for many endangered species. An instructing example are the wooded meadows (Estonian: puisniidud) of northern Europe. Having been widespread in cultural landscapes of Scandinavia and Estonia for centuries, today their conservation depends on “nature” protection measures.

In Matsalu Nature Reserve in western Estonia, a few wooded meadows are conserved at the moment, and as it is known that many more existed and have been abandoned, the reserve‘s administration is interested in the investigation of woodlands like Vöigaste Forest.

This study is a first inventory and assessment of the habitats, plants and plant communities found in Vöigaste Forest. Another aim was to gain better knowledge of the development of wooded meadows after abandonment, and to point out management suggestions for this part of the nature reserve.

1.2 Wooded Meadows

As definitions and figures in the literature are partly diverging, KUKK & KULL (1997) and LUHAMAA ET AL. (2001) are referred to as main sources of information.
Wooded meadows are sparse natural stands of deciduous trees and shrubs with a regularly mown herb layer. Typically, tree canopies cover 20-40% in small irregular patches of a few trees (LUHAMAA ET AL. 2001), as illustrated in Figure 1. Common species are ash (*Fraxinus excelsior*), oak (*Quercus robur*), poplar (*Populus tremula*), birch (*Betula pendula* et *pubescens*) and hazel (*Corylus avellana*).

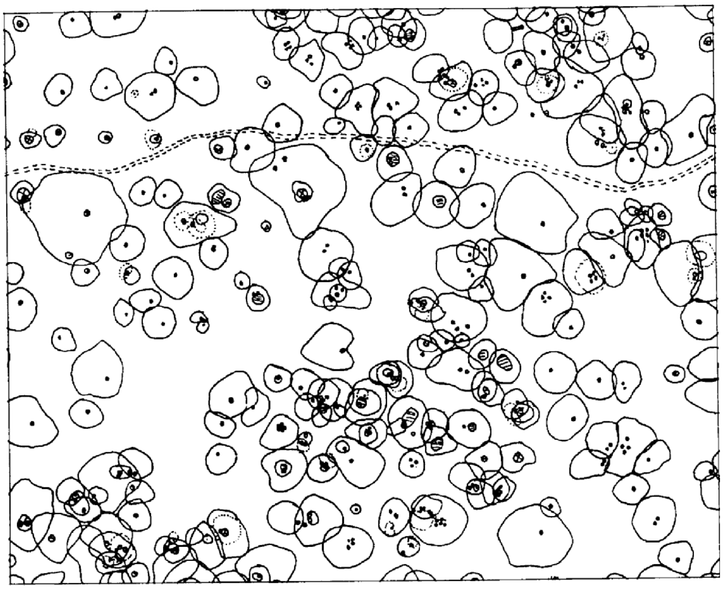


Figure 1: Treetop contours (1ha) in Laelatu wooded meadow (from Kukk & Kull 1997)

Traditional management consisted of gathering branches in spring, mowing in July, slight grazing afterwards (not always), as well as coppicing single trees for firewood and timber. Contrary to Scandinavia, in Estonia trees were not pollarded. Secondary products of these lands were e.g. berries, hazelnuts, medicinal herbs and birch sap (LUHAMAA ET AL. 2001). Multifunctional land use around human settlements had led to similar ecosystems already 4000 years ago, and when the adoption of the scythe 2000 years later allowed gaining hay for winter fodder, wooded meadows supposedly gained their characteristic appearance. When these practices were given up, overgrowing took place and usually resulted in a loss of species diversity in the herb layer (KUKK & KULL 1997, LUHAMAA ET AL. 2001).

While in other countries the area of wooded meadows was declining again earlier, their distribution in Estonia reached its maximum of approx. 850,000 ha (19% of the surface area) at the end of the 19th century, with a certain concentration in the western part of the country on calcareous soils. The abandonment of wooded meadows in the last 100 years came with reduced land management during wars, introduction of machine-mowing, land reforms and agricultural intensification under the Soviet regime. In the last decade, the decline of animal husbandry and of subsistence agriculture has continued.
(KUKK & KULL 1997)

At the same time, scientific research has intensified to document the situation of these endangered ecosystems and to analyse their biodiversity. They are a habitat for numerous rare and endangered species; maximum small-scale richness of vascular plants was found on Vahenurme wooded meadow: 74 species per m^2 (KUKK, KULL 1997).
The extraordinary species richness in the herb layer can be attributed to the levelling of competition and extraction of nutrients by yearly late mowing, the calcareous soils, to selective grazing and the heterogeneity in abiotic conditions inside the meadow,

especially the change of light and moisture conditions under and between the trees (see Figure 1). The territory of wooded meadows has been large, and they have often been in continuous, similar use for centuries, which meant long-term stability for ineffective propagators and other "sensitive" species. These diverse, well-structured ecosystems also offer suitable living conditions for a wide variety of mosses, lichens and funghi, as well as insects, birds and mammals.
(KUKK & KULL 1997, LUHAMAA ET AL. 2001)

Wooded meadows are a focus of interest for nature protection, and because only a few hundred hectares in Estonia are regarded as still intact (KUKK & KULL 1997), restoration is attempted on abandoned and overgrown sites.

According to KUKK & KULL (1997), different aspects of wooded meadows have been used for classifications, e.g. cultivation techniques, state of abandonment, soil acidity, water regime, plant communities, or combinations thereof. For western Estonia it can be summarised that wooded meadows occurred mainly on calcium-rich soils, wet and dry spots were alternating, trees were coppiced, and typical plant community types were *Hepatica-Pulmonaria*, *Sesleria caerulea-Filipendula vulgaris, Scorzonera-Melampyrum* (KUKK & KULL 1997).

2 Study Area

2.1 Location

The study site belongs to Matsalu Nature Reserve (see History, p. 8) in western Estonia, Läänemaa. Matsalu Bay is a shallow bay of the Baltic Sea, with the Kasari river flowing into it. Võigaste Forest (Võigaste Mets) covers approximately 700 ha (7 km^2) of woodland south of the bay (about 58°42´ N and 23°37´ E), between the villages of Metsküla, Meelva and Salevere (see Figure 2).

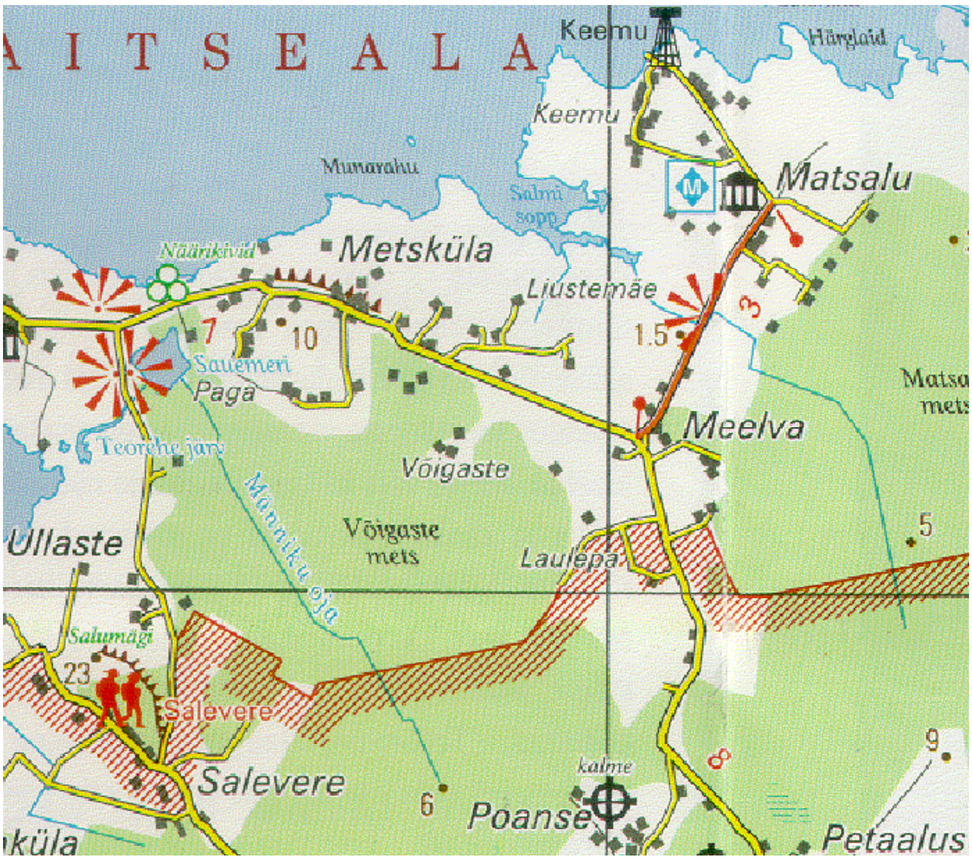
For comparison with intact wooded meadows, two sites outside of Võigaste were investigated: Allika wooded meadow (9 km east, inside Matsalu Nature Reserve) and Laelatu wooded meadow (13 km south, different nature reserve). They are comparable to the study site as far as soil and climate are concerned.

(MATSALU INFO MAPS 1990, 1998)

(Map:© www.takebreath.com)

Figure 2: Map Matsalu

(from Info Map 1998)



2.2 Geology

In the west-Estonian lowland, silurian limestone is the dominant bedrock, covered with up to 3 m of moraine and silty sediments from the glacial period. The land uplift since that time has been 3 mm per year so that the coastline is changing continuously, and part of the coastal lowlands have been under human influence since their emergence from the Baltic Sea (LOTMAN 1998, LUHAMAA ET AL. 2001). The study area lies >1 km inland at 5-10 m above sea level (KINK 1996) and is thus hardly influenced by salt water.

2.3 Climate

The region's northern European climate is mitigated by the vicinity to the Baltic Sea and the Atlantic Ocean. With a mean annual temperature of 6°C (-4°C in January, 17°C in July) and mean annual precipitation of 650 mm (2/3 in summer) at the meteorological post Virtsu, close to Matsalu bay, the climate can be characterised as atlantic-continental, with warm summers, moderately mild winters and a growing season of 6 months.
(KINK 1996, LUHAMAA ET AL. 2001)

2.4 Soils

Due to the limestone bedrock, the study area is dominated by neutral and slightly calcareous soils. Their depth is varying with the thickness of the sediment layer; bedrock outcrops and erratic boulders are common.
(LUHAMAA ET AL. 2001)
The groundwater table is 0-2 m below surface and fluctuating significantly during the year (up to 2 m): large parts of Vöigaste Forest are flooded in winter and spring, but especially open grasslands can dry out quickly in summer. Gleyzation, leaching, paludification and peat accumulation in mires are widespread.
(LUHAMAA ET AL. 2001, LOTMAN 1998)

2.5 Flora and fauna

On the global scale, western Estonia belongs to the northern mixed forest zone (hemiboreal vegetation). A significant difference to central European forests is the absence of beech (*Fagus sylvatica*), which is replaced by hardwood trees like ash (*Fraxinus excelsior*), maple (*Acer platanoides*), lime tree (*Tilia cordata*) and elm (*Ulmus spp.*). Oak (*Quercus robur*), birch (*Betula spp.*) and alder (*Alnus spp.*) are also common. (DIERßEN 1996) Due to its geographical position and proximity to the sea, several phytogeographic groups are mingling here, e.g. arctic-alpine, subatlantic, boreal and nemoral species. Matsalu wetland has been affected by human activities since prehistoric times; this has included mowing, grazing, tree felling and reed harvesting.
(LUHAMAA ET AL. 2001, LOTMAN 1998)

These influences, together with the abiotic conditions, have produced a high variety of natural and semi-natural habitats and thus a remarkable species richness: For Matsalu wetland 700 species of vascular plants are recorded, as well as 260 species of birds, 48 of mammals and 40 of fish (MATSALU INFO MAP 1990). KALJUSTE (2001) states that many of these are not rare in Estonia, but endangered in neighbouring countries and included in the Red Data Book of the Baltic Region. Matsalu is included in the “Ramsar” list of wetlands, due to its international importance as a resting place for several 100,000 migrating birds and nesting site for many endangered species (www.ramsar.org).

Vöigaste Forest can be characterised mostly as a wet deciduous forest, but it includes semi-open woodland and open grassland in different successional stages after abandonment. Being not of primary interest in the Matsalu bird sanctuary, no specific research on flora or fauna of this area had been done prior to this study.

2.6 History

The region had been dominated by small-scale agriculture, until major dredging activities and Soviet land reforms took place in the 20th century. The natural conditions were not suitable for intensive land use, though, and the last 50 years have witnessed migration into the cities and a gradual abandonment of traditional practices and semi-natural habitats. Ornithological interest had focused on Matsalu bay already in the 1870’s, and in 1957 the Matsalu State Nature Reserve was founded.
(LOTMAN 1998)
The reserve comprises 48,640 ha, of which more than half are covered by water. Important habitats are further: reedbeds (3000 ha), islets, flood plains, coastal meadows, forests and wooded meadows (KALJUSTE 2001). Active man-induced threats include drainage and fertilisation, but they are surpassed by the passive threats of abandonment and overgrowing of pastures and meadows. According to LOTMAN (1998), present conservation efforts are focusing on support for appropriate farming practices and management of the semi-natural meadow communities, most of all mowing and grazing. Regular patrolling and monitoring are carried out.

Vöigaste Forest is mostly uninhabited today and belongs partly to the limited management zone of the nature reserve, where restricted forestry activities are allowed. This concerns mainly the exploitation of firewood, which is still the main heating material in Estonia. In former times, part of the forest was extensively used as (wooded) meadows, pastures and fields.

3 Material and Methods

3.1 Basic information material

The following cartographic material was available for Vöigaste Forest:
General map 1:20,000 (based on older information, date unknown)
Forest map 1:10,000 (1990) (included in appendix)
Soil map 1:10,000 (1980)
Aerial photo (1999)

Data about Estonian vegetation, Matsalu Nature Reserve and wooded meadows was partly found in publications written in Estonian, of which only summaries were available in English, so that information may be incomplete. Interviews with the nature reserve administration added details, but much knowledge about the land use history of the different parts of Vöigaste has been lost in the past.

3.2 Field work

For vegetation analysis, the phyto-sociological method after BRAUN-BLANQUET (1964) was used, which can only be roughly described here (see References for details).
The method aims at a characterisation of a stand of vegetation by a combined cover-abundance estimation of each species within a defined, representative and uniform sample plot. The following scale is used:

r: one or few individuals
+: covering less than 1% of the plot area
1: covering 1-5%; if less, then very abundant (i.e. many individuals)
2: covering 5-25%; if less, then very abundant
3: covering 25-50%
4: covering 50-75%
5: covering more than 75%

More details regarding the occurring plants can be recorded, but were left out in this case. The data is taken separately for each stratum of vegetation (e.g. field layer, bushes, several layers of trees), and height and total coverage of each layer is recorded. Additional parameters and observations are included according to relevant questions; the resulting comprehensive analysis of the plot is called relevé ("Aufnahme").

In the classificatory approach after Braun-Blanquet, the vegetation samples are thus characterised floristically and then grouped into phyto-sociological units.

For this study, relevés in Vöigaste Forest were carried out in June and July 2002, on squares of usually 100 m^2 in forests and 50-80 m^2 in open grassland. These are described as adequate plot sizes for example by PFADENHAUER (1997) and were checked in the field. Only vascular plants were inventoried. The bryophyte layer coverage was not noted everywhere and not analysed any further.
For identification of the plant species, mainly SCHMEIL (2000), ROTHMALER (2000) and KLAPP (1990) were used (others: see References). Nomenclature is referring to SCHMEIL (2000).

The placement of the relevés was chosen from the forest map with the aim to sample mainly abandoned wooded meadows, although this proved to be problematic (see Forest map, p.13). At each site, UTM (Universal-Transversal-Mercator) co-ordinates were taken for exact location (± 10m), and light conditions were characterised with the help of a horizontoscope. The horizontoscope is used to determine a spot's potential hours of direct sunlight per growing period, taking into account the geographic latitude, the month and any shadow-casting objects around. For relevés 1 to 27, an inlay sheet of 53° latitude was used, which was then replaced by the more appropriate one of 60°. This exchange implies a certain error, which was estimated to be 6% at the most. As this is less than the variation within one plot, the error is considered negligible.

Soil types were determined as far as possible at the beginning of the study, but later were adopted from the soil map. Additional relevés were made in two still intact wooded meadows (see Location, p.6) for comparison with the overgrown sites in Vöigaste. In order to analyse the small-scale variation in the field layer of wooded meadows, a transect was made on Laelatu wooded meadow, covering dark and light spots under and between trees.

3.3 Statistical evaluation

The first step in analysing the vegetation was to calculate the average Ellenberg indicator values for each relevé. ELLENBERG ET AL. (1991) derived indicator values of plant species for each of the following parameters:

- Light
- Temperature
- Continentality
- Moisture
- Reaction (pH)
- Nutrients

The numerical values range in each case from 1 (parameter weak/low) to 9 (parameter strong/high), only for moisture they extend to up to 12 (always under water surface). From these figures, the abiotic habitat conditions of a given plant community can be derived approximately. These indicator values have originally been validated for central Europe only, so their application in other regions is critical. Furthermore, it is mathematically incorrect to calculate average indicator values since they represent an ordinal and no metric scale. As in similar cases, calculations were carried out nevertheless, but the results interpreted carefully.

Here, the average indicator values of relevés were calculated in two different ways for methodological comparison:

a) qualitative means: species not weighted
b) quantitative means: species weighted according to their per cent coverage, using the following transformation: r – 0.1%, + - 0.2%, 1 – 2.5%, 2 – 15%, 3 – 37.5%, 4 – 62.5%, 5 – 87.5%.

For detailed explanations see ELLENBERG ET AL. (1991).

With the help of indicator values, light conditions and observations in the field, the relevés were grouped in order to generate distinct vegetation formations, i.e. plant associations. This classification was supported by arranging the original data in tables, and identification of common and characteristic species of each community according to the Braun-Blanquet approach.

As the syntaxonomic nomenclature after Braun-Blanquet is not consistent within Europe and hardly applicable to the special case of wooded meadows, plant communities in this study were distinguished and named by a combination of physiognomic and floristic features. These communities are treated as units of classification, and only a rough comparison is made to phyto-sociological nomenclature (see p.36).

For comparison of indicator values, species numbers and plant communities, different graphic representations were used.
Apart from this classification by various parameters, which must to a certain extent be subjective, the relevé data was submitted to a pair-wise hierarchical cluster analysis (program SYSTAT). For this strictly mathematical comparison, only presence or absence of field layer species occurring in more than 9% of the relevés was considered. As similarity measure for each pair of relevés, the Jaccard index was used. It is defined as:

$$\mathrm{J} = \frac{c}{a+b+c} * 100\%$$

with c the number of common elements (here species) and a and b the number of elements found only in one of the relevés (TREMP 2002). The more similar two relevés are, the higher is their Jaccard index, and after analysis of all pairs of relevés, results are displayed in a tree diagram.

4 Results

4.1 Maps

The cartographic material provided valuable information about the study area, although exact localisation in the field was only roughly possible, as no map co-ordinates were available. The choice of sites presented a number of problems: The total area of 700 ha was very heterogeneous, not easily accessible and not well mapped, so that a complete coverage of the area was not possible in the given time.

4.1.1 Forest map

The forest map is included in the appendix for comparison.
Relevés concentrated on the plots characterised as (old) wooded meadows in the map (vertical striped plots), as well as on open patches recognisable on the aerial photo. During the field work it became obvious that the forest map information was in part incorrect, and the marked plots included not only wooded meadows in all stages of abandonment, but also closed forest and open landscape without resemblance to wooded meadows. Often different plant communities could be found even within one plot. Additionally, the forest map concentrates on dominant tree species and age classes, whereas plant communities of this study were characterised mostly by their field layer composition.

After visiting and taking relevés in all wooded meadow plots and a number of others, the results are strictly true only for these sites. However, from the observations made while passing through almost all parts of the area in the course of the study, it can be assumed that the formations found and described by the relevés are representative for Vöigaste.

4.1.2 Soil map

As an Estonian classification was applied in the soil map (not compatible to the German or FAO system), no soil type names were used here, but only their basic information extracted.
In general, the soils of Vöigaste are neutral and situated on limestone, the mineral layer consisting mostly of sandy silt loam. They are often soddy and show gleyic properties. In places they are stony with a thin organic layer on the bedrock, in other parts slightly acidic with peat accumulation (fen / mire). These latter types are the only ones clearly associated with certain plant communities, which is explained below (Description of plant communities, p. 16). For the use within Matsalu Nature Reserve, the abbreviations used in the soil map are included in the differentiated table of plant communities in the appendix.

4.2 Vegetation relevés and plant species

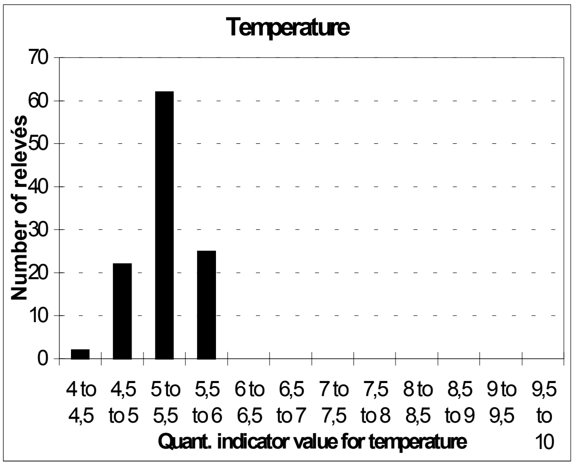
In total, 115 vegetation relevés were made, of which four are only species lists (i.e. without coverage estimation), but were analysed similarly, as far as possible. The approximate position of each relevé can be determined from its forest map plot number (see Appendix, differentiated table). There is also a list of their UTM co-ordinates for exact location.

Species identification presented a number of problems, especially in the case of plants that were not flowering yet / any more, or that formed only vegetative sprouts in the shade, e.g. *Brachypodium, Lysimachia, Carex, Viola, Salix*. Individuals and taxa that could not be identified reliably were not listed in the differentiated table and left out of all analysis. The resulting species list of Vöigaste Forest contains 335 species of vascular plants, of which 10 were only found by R. Böcker in April 2002 (see Appendix). 13 taxa of these are considered to be threatened in Estonia and placed under protection, as will be described in more detail below (Occurrence of protected species, p. 30). Species only found in relevés on wooded meadows outside Vöigaste, as well as ruderal and cultivated species on agricultural land, are not included in the list.

As there are approx. 770 vascular plant species occurring in Matsalu Nature Reserve (KALJUSTE 2001), half the flora of Matsalu Bay can be found in the study area of Vöigaste, although it lacks many typical habitats (coastal meadows, reedbeds, open water, etc.).

4.3 Indicator values

The Ellenberg indicator values of relevés gave a first impression of the differences between habitats and plant communities.



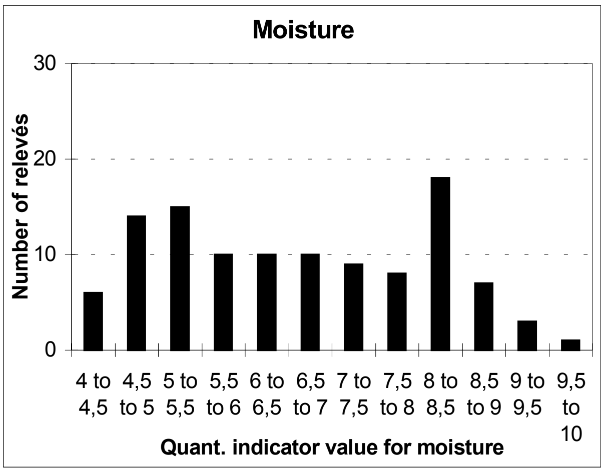


Figure 3: Distribution of Ellenberg indicator values (examples)

Throughout this study, only quantitative values were used, because their greater dispersion allows more detailed interpretation than qualitative values. With the same intention, the values for temperature and continentality were left out of consideration, as they varied much less than, for example, moisture values (see Figure 3). While the numbers for temperature show a narrow range from 4 to 6, those for moisture are dispersed more evenly, with two slight peaks at 5 (medium moisture) and at 8 (often wet).

In the case of the values for light, a modification seemed appropriate: Comparing indicator values to the horizontoscope data (sunshine hours) and to the total coverage of trees and shrubs, it was found that indicator values only varied very little. On the other hand, sunshine hours and coppice cover correlated satisfyingly (see Figure 4), so that the sunshine hours were used instead of indicator values for most of the following calculations.

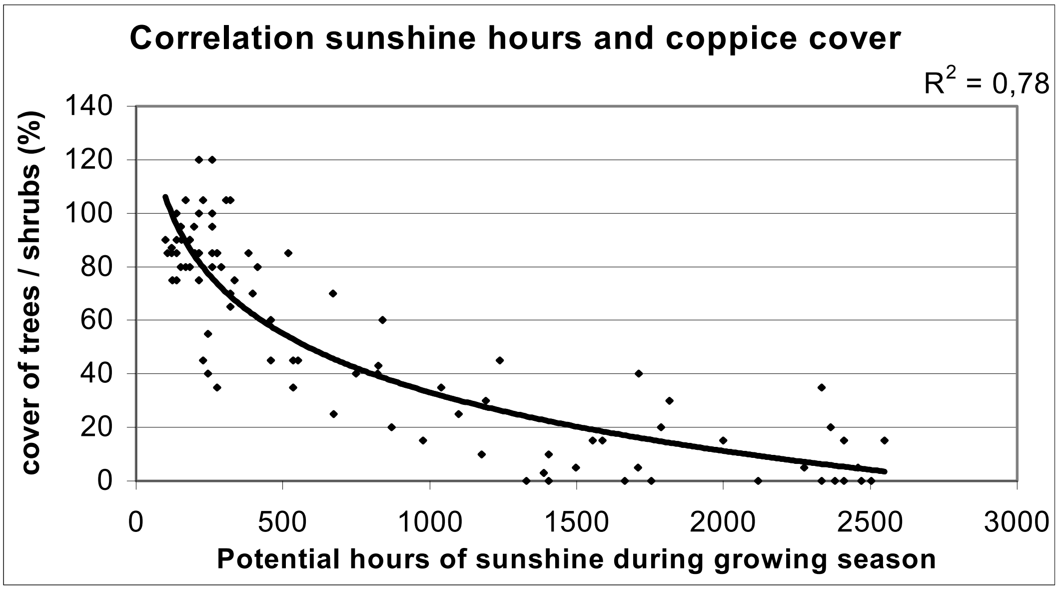


Figure 4: Correlation sunshine hours and coppice cover (%)

4.4 Description of plant communities

The combination of the parameters described above facilitates the grouping of the 115 relevés into 11 distinguishable plant communities. They are not defined solely by their species assemblage, but also by the physiognomic structure. The latter is important for theories on succession, as well as for the assessment of animal habitat qualities and other nature conservation aspects. Figure 5 shows the overview of plant communities, each with dominant and characteristic species. The plant community names were derived from the vegetation rather than from the soil properties, so not all relevés of groups C and D may meet soil scientists' definitions of "fen". Three main groups were derived: open land, semi-open landscape with scattered (groups of) trees (cover 10-50%) and closed canopy forest (cover >50%). Within these groups, plant communities were ordered according to the degree of moisture, which proved to be the most varying and meaningful parameter after light conditions.

On the following pages, each plant community will be described in detail with focus on physiognomy and on characteristic species. Therefore, not all dominant species listed in the table may be mentioned again (e.g. *Convallaria majalis*), and other widespread but uncharacteristic species are mostly left out of consideration (*Filipendula ulmaria, Potentilla erecta, Geum rivale, Galium boreale, Maianthemum bifolium, Melampyrum nemorosum, Fraxinus excelsior, Quercus robur*, etc.). Average indicator values are later contrasted in various diagrams for clarification (see Comparison of plant communities).

Overview plant communities in Võigaste Forest

	NAME	TREES	SHRUBS	DOMINANT SPECIES (field layer)	CHARACTERISTIC SPECIES (field layer)	
A	Alvar grassland	---	*Juniperus communis* *Rhamnus cathartica*	*Helictotrichon pratense* *Sesleria caerulea* *Filipendula vulgaris*	*Plantago media* *Anthyllis vulneraria* *Pimpinella saxifraga*	Open land
B	Moist grassland	---	*Frangula alnus* *Populus tremula* *Betula pubescens*	*Galium boreale* *Inula salicina* *Centaurea jacea*	*Scorzonera humilis* *Anthoxanthum odoratum* *Carex pallescens*	
C	Temporarily wet rich fen	---	*Frangula alnus* *Salix cinerea* *Betula spp.*	*Molinia caerulea* *Carex panicea* *Sesleria caerulea*	*Carex hartmanii* *Carex davalliana* *Primula farinosa*	
D	Permanently wet rich fen	---	*Frangula alnus* *Alnus incana*	*Carex elata / lasiocarpa* *Lysimachia vulgaris* *Molinia caerulea*	*Carex flava* *Potentilla palustris* *Eriophorum angustifolium*	
E 1	Abandoned wooded meadow, dry	*Populus tremula* *Quercus robur* *Fraxinus excelsior*	*Frangula alnus* *Corylus avellana* *Populus tremula*	*Calamagrostis epigejos* *Convallaria majalis* *Brachypodium pinnatum*	*Hepatica nobilis* *Dactylis glomerata* *Mercurialis perennis*	Semi-open land
E 2	Abandoned wooded meadow, wet	*Populus tremula* *Quercus robur* *Fraxinus excelsior*	*Frangula alnus* *Populus tremula* *Fraxinus excelsior*	*Calamagrostis epigejos* *Convallaria majalis* *Brachypodium pinnatum*	*Aegopodium podagraria* *Deschampsia cespitosa* *Geum rivale*	
F	Temporarily wet rich fen, overgrowing	*Betula pubescens* *Populus tremula*	*Frangula alnus* *Salix cinerea* *Betula spp.*	*Molinia caerulea* *Carex panicea* *Lysimachia vulgaris*	*Carex hartmanii* *Cirsium heterophyllum* *Inula salicina*	
G	Hardwood forest	*Quercus robur* *Corylus avellana* *Tilia cordata*	*Corylus avellana* *Tilia cordata* *Sorbus aucuparia*	*Convallaria majalis* *Anemone nemorosa* *Mercurialis perennis*	*Acer platanoides* *Viola mirabilis* *Polygonatum spp.*	Closed Canopy
H	Wet deciduous forest	*Betula pubescens* *Fraxinus excelsior* *Alnus glutinosa*	*Frangula alnus* *Fraxinus excelsior* *Alnus glutinosa*	*Convallaria majalis* *Filipendula ulmaria* *Rubus caesius*	*Cirsium oleraceum* *Trollius europaeus* *Phragmites australis*	
J	Swamp forest	*Alnus glutinosa* *Alnus incana* *Fraxinus excelsior*	*Alnus incana* *Alnus glutinosa* *Frangula alnus*	*Filipendula ulmaria* *Deschampsia cespitosa* *Rubus caesius* *Scutellaria galericulata*	*Lycopus europaeus* *Galium palustre* *Lythrum salicaria* *Iris pseudacorus*	
K	Intact wooded meadow	*Fraxinus excelsior* *Quercus robur* *Betula spp.*	*Corylus avellana* *Fraxinus excelsior* *Quercus robur*	*Convallaria majalis* *Melampyrum nemorosum* *Scorzonera humilis*	*(Ohioglossum vulgatum)* *(Dactylorhiza spp.)*	Semi-open wooded meadow

Figure 5: Plant communities

4.4.1 Alvar grassland (A)

"Alvar" is a common northern European expression for meadows with a shallow humus layer on limestone (LUHAMAA ET AL. 2001). They often support a calcareous grassland, which in Vöigaste Forest is dominated by graminoids like *Helictotrichon pratense, Sesleria caerulea, Carex tomentosa*, as well as *Primula veris, Galium boreale* and *Filipendula vulgaris*. These herbs indicate a cessation of mowing or grazing, which results in the growth of *Juniper, Rhamnus* and other shrubs and suppresses more delicate, typical herbs like *Anthyllis vulneraria, Medicago lupulina, Polygala amarella, Pimpinella saxifraga*.

It is important to know that alvars, despite their aridity in summer, can be soddy in winter and spring. This is reflected by the indicator value for strong changes in water regime (~) of many species: *Helictotrichon pratense* (3~), *Carex tomentosa* (7~), *Filipendula vulgaris* (3~), *Galium verum* (4~), *Trifolium montanum* (3~). The relevés' average indicator values further show low nitrogen availability (2.8), together with a high carbonate content (7.6).

4.4.2 Moist grassland (B)

Although this group integrates communities of large meadows and small forest clearings and species composition is varying, it can be treated as one formation. There are no species growing here exclusively, but the plant community presents a high diversity due to combination of species found in neighbouring forest (*Angelica sylvestris, Filipendula ulmaria, Rubus caesius*) and open land (*Campanula glomerata, Chrysanthemum leucanthemum, Alchemilla vulgaris*).

The highest relevé species number (57) in Vöigaste was found in this community. Where human influence has ceased, some herbs start to dominate (*Galium boreale, Inula salicina, Centaurea jacea, Melampyrum nemorosum*), and shrubs and trees can spread fast (*Salix spp., Frangula alnus, Populus tremula*). In some cases, especially inside the forest, strong browsing of shrubs (at approx. 1m height) was observed and it is postulated that mammals like elk and roe deer contribute to keep these clearings open. Soils are deeper and more humid than on alvars and can be leached of free carbonates. Nitrogen availability is higher (4.4).

4.4.3 Temporarily wet rich fen (C)

This mesotrophic habitat is again characterised by fluctuations of the groundwater table, but moisture is much higher than in (A), and the drop of oxygen content in the soil allows peat accumulation. This leads to a rather low nutrient availability (value 3.3).

The plant community is dominated by *Sesleria caerulea* and different *Carex* species (*hostiana, panicea, hartmanii*) in spring, until shoots of *Molinia caerulea* appear in July. Several other plants are less common, but very specific for these calcareous fens and again indicators of the oscillating water table: *Carex davalliana, Primula farinosa* (8~), *Gymnadenia conopsea* (7~), *Epipactis palustris*, *Pinguicula vulgaris, Parnassia palustris* (8~). The habits especially of the grasses result in a very uneven ground, where tussocks provide habitats for species less adapted to wet soil, and also for shrub sprouts. Although overgrowing can be slowed by the humidity (Pfadenhauer 1997), it is not stopped, and together with tall forbs (*Lysimachia vulgaris, Filipendula ulmaria, Phragmites australis*) there are *Betula pubescens, Frangula alnus, Alnus incana* and *Salix spp*. invading.

The definition of (C), (D) and (F) as fen does not imply the exact soil properties, but the formations were named after their plant communities, in accordance with literature (esp. DIERßEN (1996), see p.36).

4.4.4 Permanently wet rich fen (D)

This plant community resembles (C) to a certain extent, but is distinguished by its permanently wet soil; in places there is open water throughout the year. There is a well decomposed peat layer (10 to 50 cm), and the upper soil can be base-unsaturated. The chemical properties are diverging, at least as far as the species can indicate. There is also a certain spatial heterogeneity within plots. On average, the soil is less calcaric than all others, and in some locations rather eutrophic (*Carex elata* dominating), in others mesotrophic (*Carex lasiocarpa* dominating).

Species numbers can be very low (8 and 9 on 25 m^2). *Molinia caerulea, Carex panicea* and some tall forbs are present, but also specialists of flooded and nutrient-poor habitats: *Peucedanum palustre* (9=), *Potentilla palustris* (9=), *Menyanthes trifoliata* (9=), *Eriophorum angustifolium* (9=), *Carex nigra et flava*, *Rhynchospora spec*. Shrubs are similarly restricted: Only *Alnus incana* and *Frangula alnus* are common.

The following plant formations (E and F) are treated separately from grassland and forest because of their physical resemblance to wooded meadows (scattered trees). Although there are no species restricted to these habitats, the physiognomy and species composition is different and justifies separate consideration.

4.4.5 Abandoned wooded meadow (E)

In some parts of Vöigaste Forest, the wooded meadow structure is still clearly visible: single old oaks, birches and aspen, stands of hazel and open grassland patches in between. Tree coverage is 20 to 50%. Yet, *Frangula* and *Populus* shrubs are coming up and the field layer is largely dominated by vigorous *Calamagrostis epigeios* and *Brachypodium pinnatum* shoots, often covering more than 50% of the area. Beneath, shade tolerant *Convallaria majalis* and *Aegopodium podagraria* are widespread, and many grassland species are “fighting for survival”. There is a clear zonation along the light gradient under and between trees. This small-scale heterogeneity was mentioned above as a typical feature of wooded meadows, and it is illustrated below by a transect in Laelatu wooded meadow (see p. 23). Soils in this formation are mostly gleyed and soddy.

The relevés were subdivided according to humidity (E 1 and E 2):

Dry variant (E 1)
This plant community shows the highest average species richness (42), which can be explained by the moderate humidity, the mosaic of light conditions and the impact of mowing until recently. Characteristic species in contrast to E 2 and F are the same as for hardwood forest (see below): *Lathyrus vernus, Hepatica nobilis, Mercurialis perennis, Platanthera spp. Tilia cordata* and *Corylus avellana* are common woody species.

Wet variant (E 2)
While there is no difference in structure between the variants, the species spectrum here is shifted towards moisture indicators: *Carex acutiformis, Cirsium oleraceum, Geum rivale, Deschampsia cespitosa*. In the two relevés where *Phragmites* is present, it shows high coverage. *Alnus glutinosa* is common.

4.4.6 Temporarily wet rich fen, overgrowing (F)

This plant community is corresponding to the rich *Molinia*-*Carex*-fen (C), but the stands here are overgrown with young birch and aspen trees (5 to 15 % coverage) up to 10m high. According to the forest map, these trees should be 40-50 years old, possibly indicating the time of abandonment. As much as 30 % of the area are further covered with shrubs (*Frangula alnus, Betula spp., Salix spp.*), and more fallow and shade-tolerant species than in (C) are present: *Inula salicina, Centaurea jacea, Angelica sylvestris, Calamagrostis epigeios, Cirsium heterophyllum, Succisa pratensis, Convallaria majalis, Fraxinus excelsior*. There are signs of browsing as well, but it does not suffice to prevent the growth of shrubs.

Forest communities in this study generally show a tree coverage over 50 %, trees are not standing in groups (as in (E)), and the field layer receives less than 500 hours of direct sunshine per growing period. In all forest formations there are parts where the tree and shrub layer is so dense that it is not possible to pass, and ground vegetation is sparse (< 50 %).

4.4.7 Hardwood forest (G)

Hardwood forest is often found on slight elevations (1 to 2 m), where the soil is stony and drier than in the surroundings. *Tilia cordata* and *Corylus avellana* are characteristic tree species, while *Alnus* and *Betula* are rarer than in other parts of the forest. In the field and shrub layer *Acer platanoides, Crataegus rhipidophylla* and *Sorbus aucuparia* can be found regularly. Herb species are similar to formation (E 1): *Hepatica nobilis, Lathyrus vernus, Viola mirabilis, Polygonatum multiflorum*.

Under the dense tree foliage (especially *Corylus* poly-cormons), the ground vegetation is often dominated by high, vegetative shoots of a few shade-tolerant species (*Anemone nemorosa, Convallaria majalis, Mercurialis perennis, Melampyrum nemorosum)*, while the growth of shrubs is hindered. The favourable soil conditions are reflected by (relatively) high indicator values for nitrogen (average 4.9) and low ones for moisture (average 4.6).

4.4.8 Wet deciduous forest (H)

This most common forest type in Vöigaste (24 % of all relevés) displays a very variable plant community of only gradual differences, so that subdivisions were not possible. Under the mixed tree layer of ash, aspen, birch, oak and alder, shrubs are standing densely in patches where more light falls in, especially *Fraxinus excelsior, Prunus padus* and *Frangula alnus*.

The ground is often covered with *Convallaria majalis, Rubus caesius* and *Geum rivale*, out of which *Filipendula ulmaria* and *Angelica sylvestris* shoots are rising. Woody species are also very common in the field layer, most of all *Fraxinus excelsior*, but also *Prunus padus* and *Frangula alnus*. Although a great number of species was found in the 28 relevés in this formation, there are no species strictly characteristic. In terms of species composition the wet forest corresponds to the wet wooded meadow (E 2). Species which are found regularly without being dominating are *Deschampsia cespitosa, Carex panicea, Dactylorhiza fuchsii, Trollius europaeus, Cirsium oleraceum*.

The groundwater table is high, and lower areas are flooded in winter / spring, which can be recognised by the bare ground (free of litter and mosses) even in summer. Here, numerous wetland species can be observed (*Carex acutiformis, Caltha palustris, Lysimachia vulgaris*), and locally *Phragmites* is dominating. Tussocks are frequently found around tree trunks, providing habitat for plants sensitive to overflooding, like *Sorbus aucuparia, Galium boreale* and *Maianthemum bifolium*.

Mosses are mainly occurring on stones and dead wood. On drier ground, nutrient availability is high (average value 5.2), and habitat is suitable for *Melica nutans, Crepis paludosa, Viola mirabilis, Anemone nemorosa, Aegopodium podagraria*, etc.

4.4.9 Swamp forest (J)

The clearly dominating trees in the swamp forest are *Alnus glutinosa* (wettest parts) and *Alnus incana*, with shrubs of *Frangula alnus* and *Fraxinus excelsior* underneath. The highest average indicator values for moisture (8.3) were found in this formation, where the water table is rising above the surface in winter and spring. After the peaty soil has dried, a lush field layer develops in summer, consisting of species adapted to the periodic flooding and rapid subsequent mineralisation of nitrogen. Species numbers are only 21.5 on average.

Dominant species are similar to wet variants of (H) (*Filipendula ulmaria, Geum rivale, Rubus caesius, Deschampsia cespitosa, Angelica sylvestris*), but several others are more characteristic and indicate regular flooding: *Scutellaria galericulata* (9=), *Solanum dulcamara* (8~), *Lycopus europaeus* (9=), *Mentha aquatica* (9=), *Lythrum salicaria* (8~), *Typhoides arundinacea*.

4.4.10 Intact wooded meadow (K)

The investigated original wooded meadows (Allika and Laelatu) are spatially separated from each other and from the study area, and since only two relevés are available, comparison with the communities of Vöigaste can only be made with reservation. Nevertheless, species pools are similar, and only few species are found solely on Allika or Laelatu (*Ophioglossum vulgatum, Dactylorhiza spp., Carex capillaris*). Main tree species are oak, birch, ash and hazel, standing in groups on a yearly mown meadow.

The abiotic conditions, physical appearance and even the species assemblage in the field layer are comparable to formation E 1, but with a change in proportion: There are few dominants (*Convallaria majalis, Melampyrum nemorosum, Scorzonera humilis*), and a wide variety of accompanying species, which are favoured by the competition-limiting management. The wooded meadows show a significantly higher species richness than all other formations (average 61) on the plot size of 70 to 80 m^2, which is in all probability less than the minimum area for this ecosystem.

In order to analyse the species distribution on the ground, a transect line was laid along a light gradient between trees, where sunlight varied between 100 and 900 hours per growing period. Every 20 cm, the intersecting species were registered, and the results are presented in Figure 6.

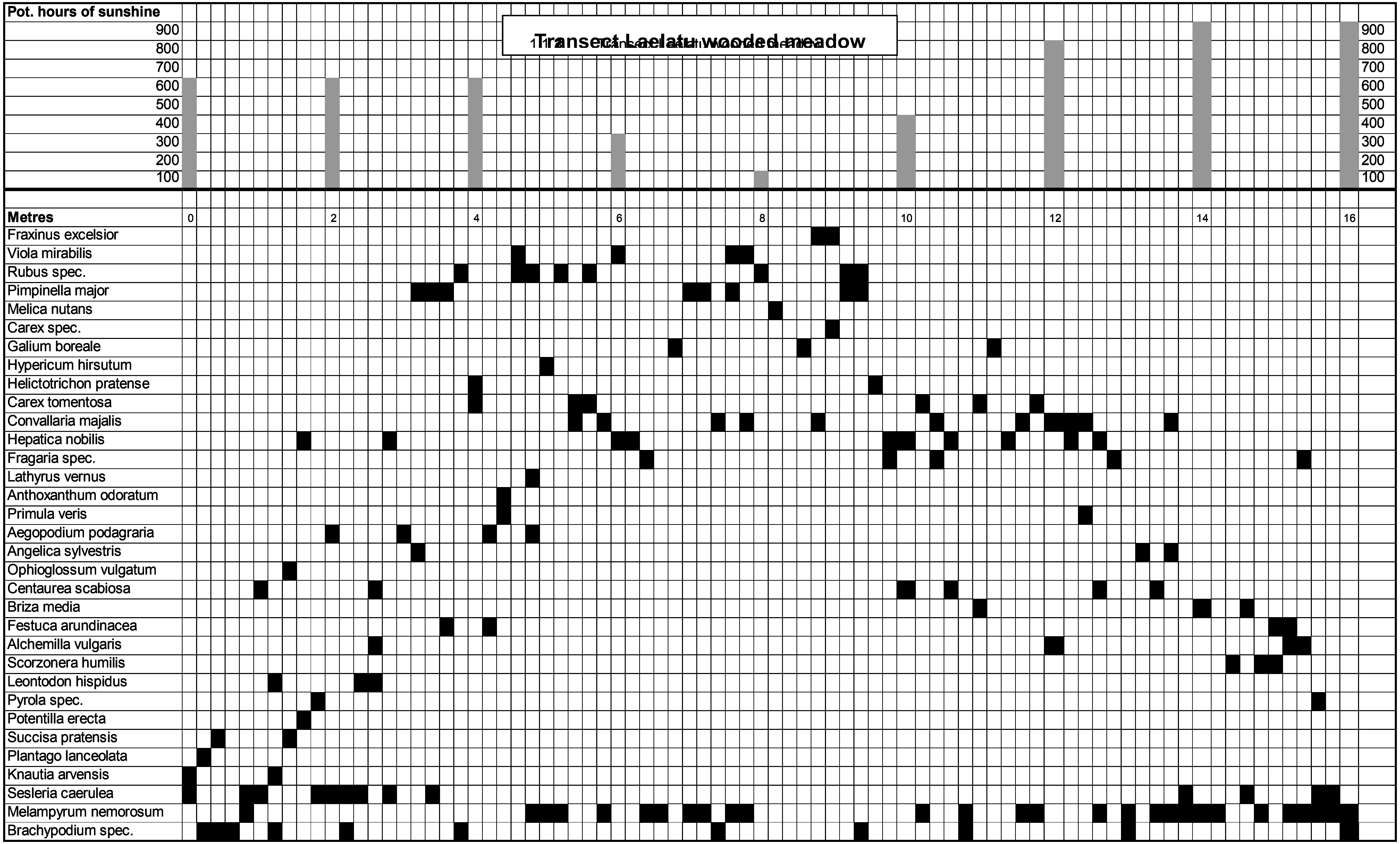


Figure 6: Transect Laelatu wooded meadow: species distribution and light conditions

The zonation of species along the light gradient (in this specific competitive situation) was already mentioned for the abandoned wooded meadows in Vöigaste (see p.20), and it is demonstrated more clearly here: Only few species are indifferent to light conditions (*Melampyrum, Brachypodium*), whereas others are restricted to open habitat (*Knautia arvensis, Sesleria caerulea, Succisa pratensis, Leontodon hispidus, Scorzonera humilis*). Species found mainly in the shade are *Fraxinus excelsior, Viola mirabilis, Melica nutans, Rubus spec*. As this light gradient occurs multiple times throughout a wooded meadow, it contributes to the field layer´s small-scale heterogeneity.

4.5 Comparison of plant communities

In the following bar charts, the 11 plant communities described above are again contrasted in their main abiotic conditions, i.e. Ellenberg indicator values for moisture, nitrogen, reaction and the potential hours of sunlight received. Standard deviations illustrate the range of parameters in each community. It should be noted that the absolute length of deviation bars is not as significant as the deviation in relation to the mean (i.e. the variation coefficient). Values for the intact wooded meadows (K) must be interpreted carefully because only two relevés are available, whereas for other formations there are at least seven.

4.5.1 Light

Although light measurements were only carried out on approx. 2/3 of all grassland plots and deviations are wide, formations can be distinguished sufficiently. Due to the region´s high latitude, sunlight can last more than 15 hours per day in open habitats. At the other extreme of a wide range, forest ground layer communities are often receiving less than one hour of sunlight per day, but variation is high due to uneven spatial distribution of trees. This is even more true for the semi-open formations (E) and (F), where average light conditions are between the two extremes, but varying intensely on a small scale.

4.5.2 Moisture

As light and moisture were the main parameters used for classification, the graphs reflect this configuration as expected: Within each group of formations of similar light conditions, the moisture indicator values are rising (from A to D, E1 to F, G to J). An exception are the fen habitats (C) and (D), where the difference is not clear. The hardwood forest turns out to be even drier than the alvar grassland. Considering the total range, no habitat can be characterised as generally dry, and the values for fens and swamp forests even indicate soddy soils with a temporary lack of oxygen.

4.5.3 Nitrogen

The soil nitrogen content as indicated by the Ellenberg values is often correlated with all major nutrients (ELLENBERG ET AL. 1991). Very few of the plant communities investigated show average values >6, which means that nowhere can the vegetation be called nitrophilous. The variation in nitrogen availability between formations is hardly wider than within them so that differences are often not significant. On average, forest habitats provide better nitrogen availability than grassland. Especially on alvars the vegetation indicates nitrogen-poorness, and to a lesser extent also in fens (C, D, F). The low values in intact wooded meadows (3.0 and 4.3) are also remarkable.

4.5.4 Reaction

The plant communities indicate a homogeneous, slightly calcaric soil throughout the studied area, with two exceptions: On alvars the influence of the limestone bedrock is reflected by a calciphilous vegetation, while the rich fen (D) shows slightly acidic soil conditions.

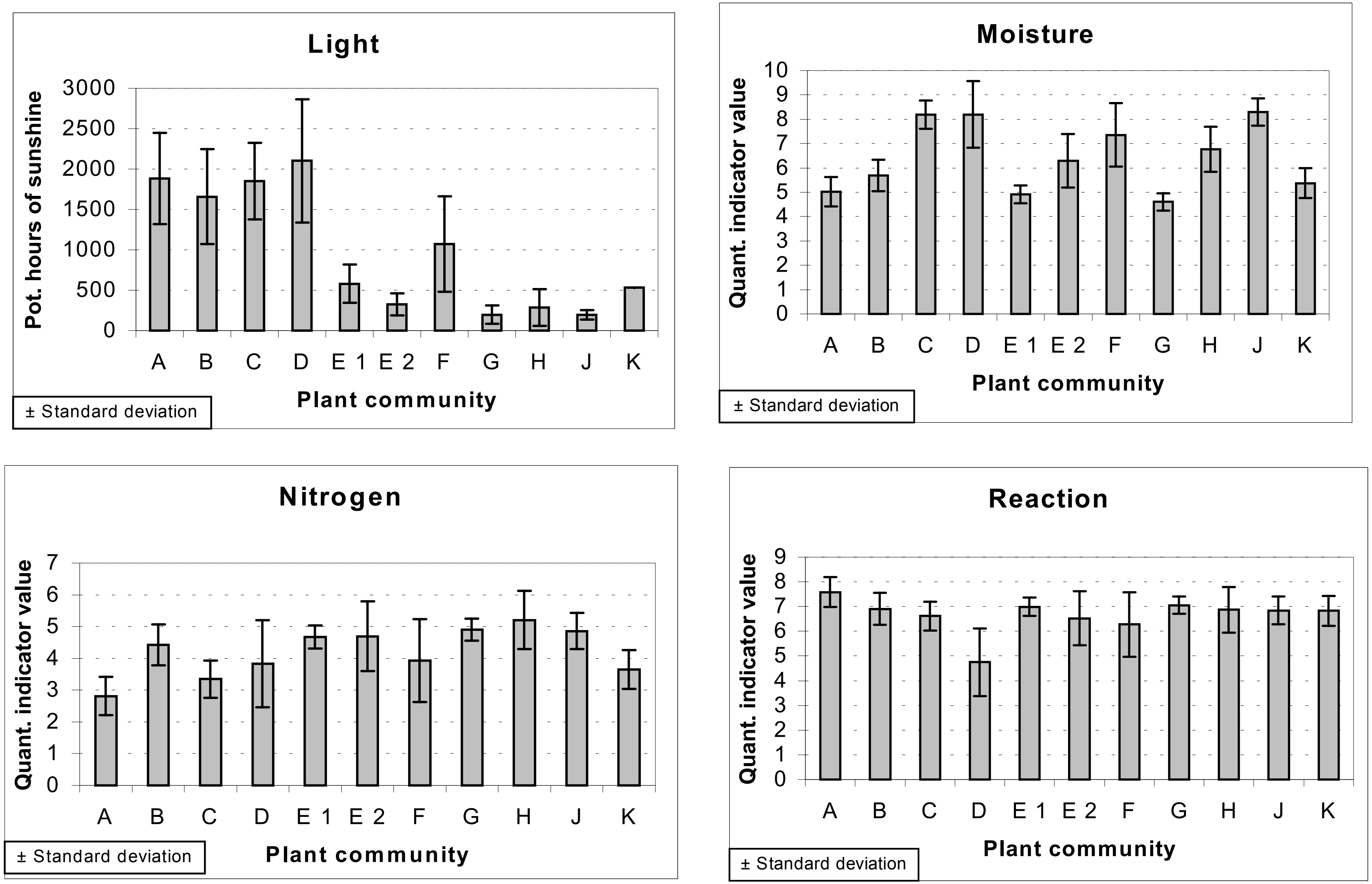


Figure 7: Indicator values of all plant communities

Plant communities: A: Alvar grassland, B: Moist grassland, C: Temporarily wet rich fen, D: Permanently wet rich fen, E 1: Abandoned wooded meadow dry, E 2: Abandoned wooded meadow wet, F: Temp. wet rich fen, overgrown, G: Hardwood forest, H: Wet deciduous forest, J: Swamp forest, K: Intact wooded meadow

4.5.5 Combination ("Ökogramm"): Light and Moisture

Taking advantage of the fact that the habitats are characterised mainly by their light and moisture conditions, as shown above, these parameters were utilised to join all plant communities in a single diagram ("Ökogramm"):

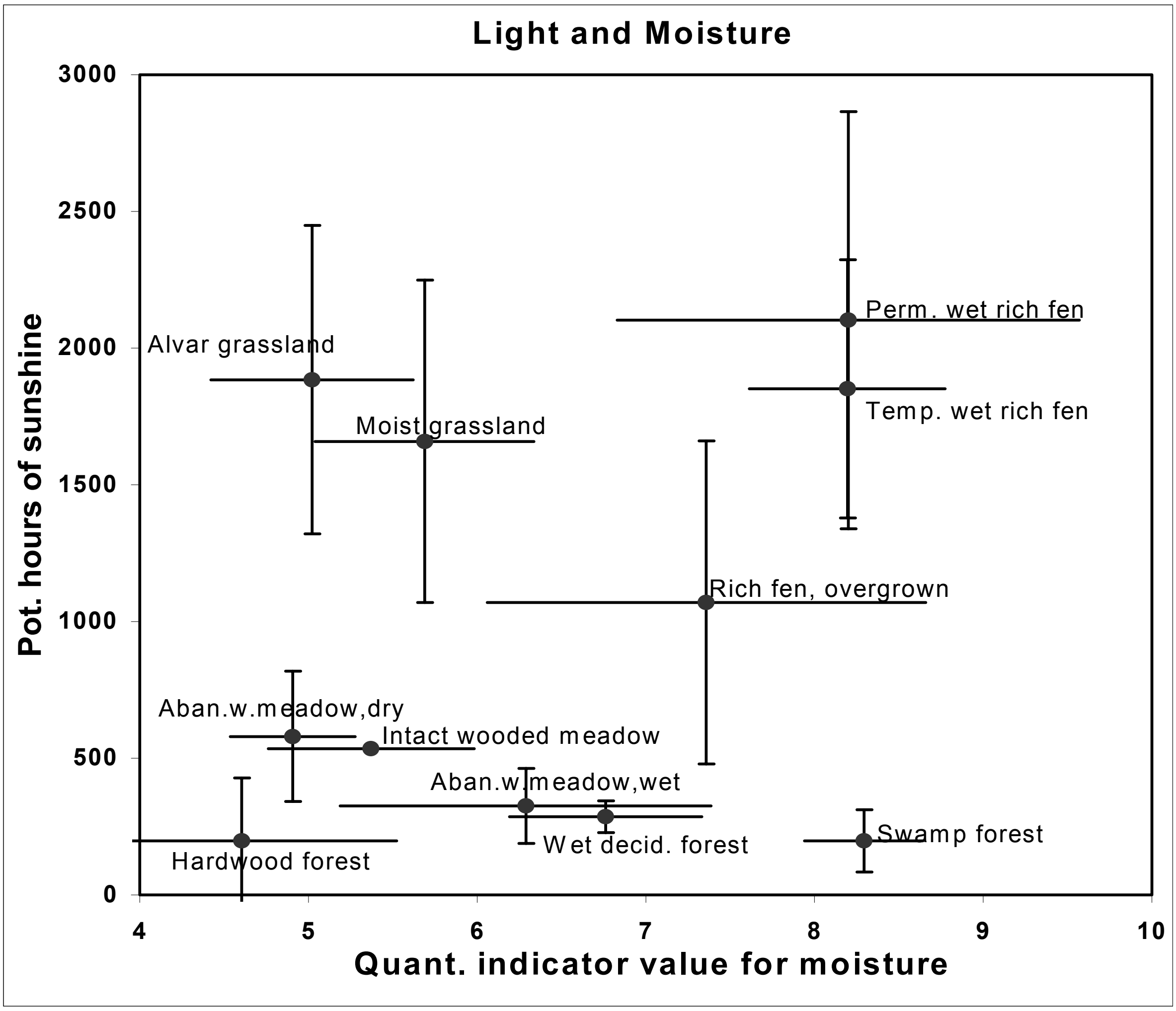
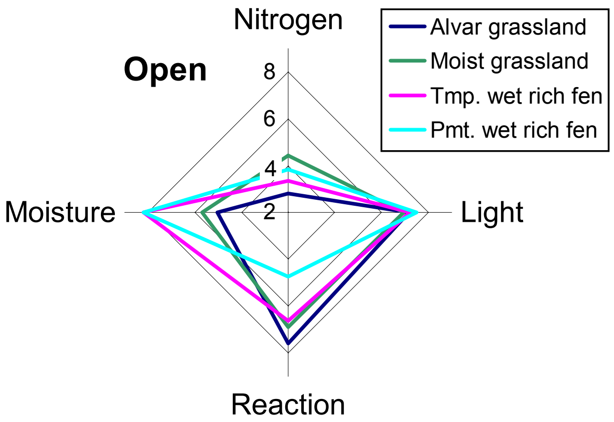


Figure 8: Light and moisture conditions in field layer

It must be noted that here only the field layer vegetation was considered. The standard deviation bars show again the wide variation within communities. The swamp and hardwood forests are distinguished clearly from all others. They represent the dry and wet extreme of the closed-canopy formations, while the wet deciduous forest lies in between and shows lighter conditions. At the other end of the scale of sunshine hours, the four open communities are well delimited from the rest, forming a drier and a more humid group (grasslands and fens respectively). The rich, overgrown fen shows less humidity than the open fen, although soil properties should be similar. The intact wooded meadow is situated next to the drier abandoned wooded meadows of Vöigaste, confirming a close relation of these communities. On the other hand, the wet variant of abandoned wooded meadows resembles the common wet deciduous forest.

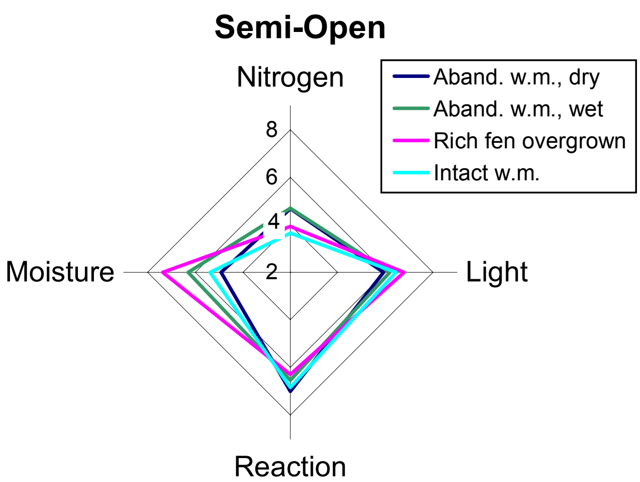
4.5.6 Condensed spectra of indicator values

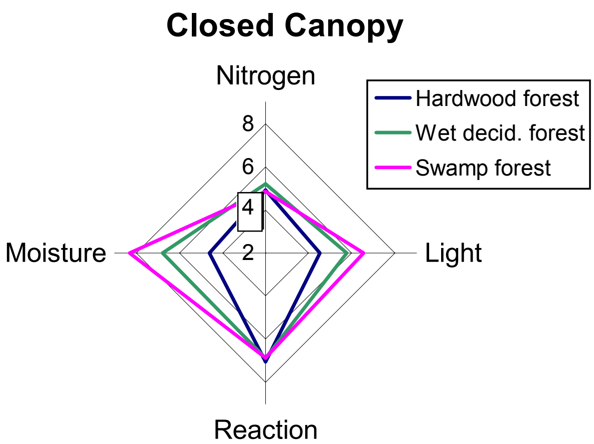
For a further comparison of all indicator values in clearer illustration, the communities' indicator values were plotted in "spider-web"- diagrams. Standard deviations were left out, and instead of sunlight hours the indicator values for light had to be used:



In the open communities the gradient in moisture has already been described; here it can be seen that the values for reaction are following he opposite trend. It is also apparent that reaction values are diverging broadly, and they are not necessarily correlated with high nutrient availability. Light indicator values show no major variation.

Light values of semi-open communities are hardly different from open land (6 to 7). The intact wooded meadow, which has been included here, is slightly wetter and less rich in nitrogen than the dry abandoned wooded meadow. Altogether, these habitats are more homogeneous than the other groups in abiotic conditions.





Under the forest canopy, the ground vegetation is supposed to show lower light values. This is found to be true for the hardwood, but not for the swamp forest, where average light values are about the same as for semi-open habitats. While the most striking differences are in moisture conditions, their possible influence on nutrient availability (mineralisation etc.) is not discernible (contrary to the open formations).

Figure 9: Condensed spectra of indicator values

4.5.7 Other plant communities

After the main plant communities have been characterised, a few comments should be made on special habitats found scattered in Võigaste Forest in the course of this study. Their territory is not large and no special relevés were made, but they contribute to the forest's diversity and can illustrate stages of transition between communities in the course of succession. Among them are *Salix* shrublands (with e.g. *Carex disticha, diandra* and *elata*, mostly found near the Männiku), dense stands of *Phragmites australis, Typhoides arundinacea* or young birches and alders.

Others are supported by past or present human land use: nitrophilous vegetation around ruins of abandoned houses (*Aegopodium podagraria* etc.), old trees on border stone walls, aquatic plants in ditches (*Typha spp., Juncus spp*.), planted stands of pine (*Pinus sylvestris*), and *Juniper* shrubs on abandoned grazed meadows. In some places, trees had been cut recently and left small openings and woody debris, and in the northern part (Metsküla), some wooded area is used for forest pasture. Additionally, the forest contains a variety of microhabitats like erratic blocks, standing and lying dead wood, sandy ant hills, waysides and forest edges, and compressed soils of vehicle tracks with accumulating rainwater.

4.6 Protected species and species richness

4.6.1 Occurrence of protected species

As mentioned above (p. 14), 13 vascular plant species found in Vöigaste Forest are protected in Estonia, out of 59 protected species in total (KUKK 1998). Three protection categories are used (LILLELEHT 1998):

I: important, very rare and highly endangered
II: rare and valuable, less endangered
III: could become threatened if picking and damaging is allowed

In the following table, the species and their protection categories are listed, together with information in which plant community they were found in Vöigaste.

Species	**Protection category**	**Plant community**
Cypripedium calceolus	III	Moist grassland, Wet deciduous forest
Dactylorhiza fuchsii	III	(various)
Dactylorhiza incarnata	III	Temp. wet rich fen
Dactylorhiza maculata	III	(various)
Daphne mezereum	III	Hardwood forest, Dry abandoned w. meadow
Epipactis palustris	III	Temp. wet rich fen
Gladiolus imbricatus	III	Temp. wet rich fen
Gymnadenia conopsea	III	(various)
Listera ovata	III	(various)
Orchis militaris	III	Temp. wet rich fen
Platanthera bifolia	III	(various)
Platanthera chlorantha	III	(various)
Viola elatior	II	Wet deciduous forest

Figure 10: Protected species in study area

Additionally, *Malus sylvestris* and *Salix repens* may be present, but could not be identified positively because of contradicting nomenclature in Estonian and German literature. Protected species were found in all plant communities but swamp forests, so that no ranking of valuable and less valuable habitats is possible. It should be noted that, apart from the 59 legally protected species, 250 more species of vascular plants are considered threatened in Estonia (LILLELEHT 1998).

4.6.2 Species richness of habitats

Species richness is a common measure of a community´s diversity, if evenness of species distribution is left out of consideration. In the graph below, average species numbers of relevés in the Vöigaste plant communities are presented:

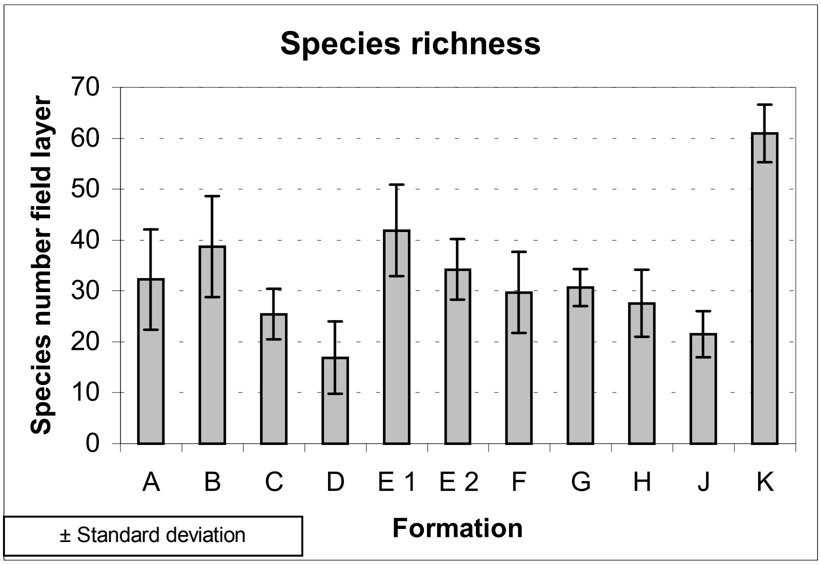


Figure 11: Species numbers of plant communities

The most obvious fact is the extraordinary high species number in intact wooded meadows. Next are dry, abandoned wooded meadows and moist grassland. On the other hand, rich fens (C and D) and swamp forests show low species richness, while all other formations are alike, taking into account the variability. However, species richness is not the only criteria in nature conservation, since for example fens are habitat of some of the protected plant species mentioned above (see Figure 10).

Searching for the parameters that may determine diversity in the study area, correlations of species numbers with all investigated parameters were tested. The only significant interrelation was found to moisture ($p<0.001$):

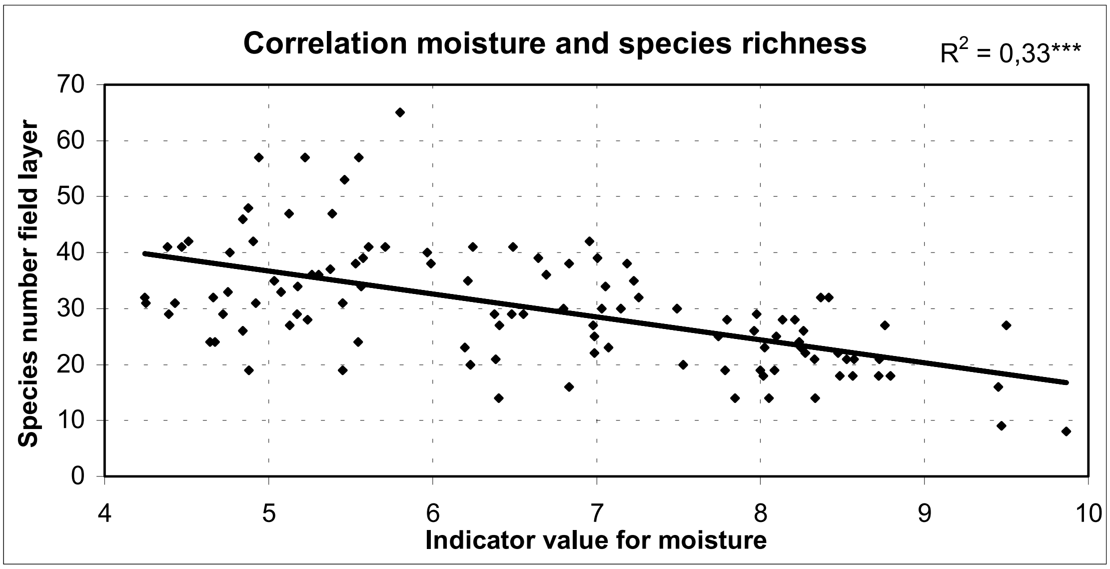


Figure 12: Moisture and species numbers

With increasing humidity, species richness is declining, but the variability especially in drier habitats indicates that moisture is not the only variable determining diversity.

4.7 Cluster analysis of relevés

The cluster analysis is interpreted in this extra chapter, because it is a strictly statistical method for calculating and illustrating similarities and was not used for the prior grouping of relevés into plant communities. Each relevé is characterised by its identification number and the plant community it was assigned to. The relevés are joined by vertical lines according to their similarity and thus are forming separate clusters (see Figure 13).
It is important to know that no absolute scale of similarity can be derived from the position of the vertical lines; the exact similarity is expressed by the Jaccard index of a pair of relevés. To give an example of this irregularity: Maximum similarity (J=64%) was found between relevés H89 and H94, which is not reflected in the cluster diagram.

The tree diagram derived in this study can give an overview of the groupings of relevés, and several clusters can be distinguished:

Formations J (swamp forest), A (alvar grassland) and G (hardwood forest) are separated clearly from others; e.g. similarity between A8 and A66 is 29%, between J57 and J114 35%, between G31 and G70 33%.
The plant communities of rich fens (C, D, F) are also clustered near each other, with C and D mixed and F at some distance (similarity between D5 and D6 is 42%, between D63 and D101 even 60%, between F12 and C104 only 12%).
Most of the moist grassland relevés (B) are clustered loosely with (A). B33, B34 and B35 should not be considered; due to an error in calculation, they show no similarity to any others.
The two intact wooded meadows (K) are rather differing from each other (J=34%) and from the neighbouring E1 and E2.
While E1 relevés (dry abandoned wooded meadow) are clustered together (between E1-40 and E1-T1: J=57%), E2 is distributed among various other formations.
Of the largest group (H), wet deciduous forest plots, the majority is grouped in the bottom cluster (H86 and H88: J=57%), suggesting a wide distance to all other relevés.

In a comprehensive view, the cluster analysis confirms the former classification of relevés.

Cluster analysis of releves

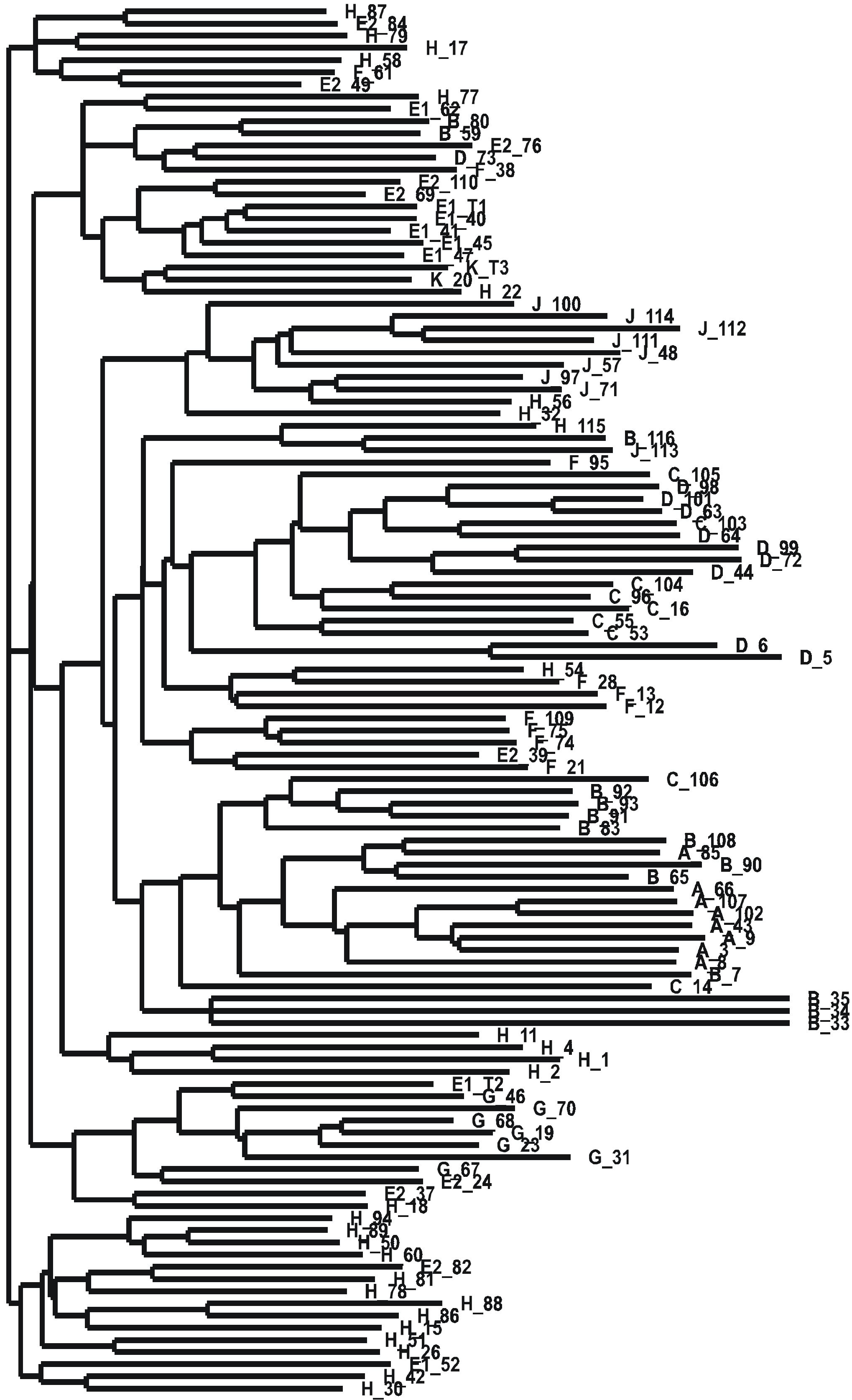


Figure 13: Hierarchical cluster analysis of relevés

5 Discussion

After methods and results have been outlined and interpreted, they will be discussed here in relation to the literature covering relevant issues.

5.1 Indicator values

Ellenberg indicator values have been initially derived for central Europe only, and they reflect the species' occurrence under the actual ecological conditions and competition with other plants. Therefore, their use in regions with different climate, different ecotypes and different competing species is problematic (ELLENBERG ET AL. 1991). In the case of western Estonia, however, climate and flora were considered sufficiently similar for the applied calculations. As mentioned before (Statistical evaluation, p. 11), calculating average values is mathematically incorrect, and data should only be used for relative comparison within this study. As values for temperature and continentality are assigned on account of a species' geographic range within the whole of Europe, no significant differences between plant communities in Vöigaste were to be expected.

Average values for moisture, reaction and nitrogen / nutrients are adequately reflecting differences in soil properties, while indicator values for light show less variation. According to ELLENBERG ET AL. (1991), there are several causes for this phenomenon: Light values for most species only range between 6 and 8, light conditions especially on the forest floor change on a small spatial scale, and many species can survive for a long time in vegetative form when light reception declines, as happens in the course of succession (e.g. *Convallaria, Maianthemum, Calamagrostis*). FISCHER AND BENS (2001) state that herbs (e.g. *Angelica sylvestris*) react more slowly than grasses. It must also be taken into account that the hemiboreal deciduous forests are not as dark as typical beech forests ("Hallenwälder") in central Europe. The potential hours of sunshine thus provide a more adequate measure of light reception although variation within a plot is not considered, either.

A similar variation in space (tussocks and hollows) and time (spring flooding) can be found for moisture, which partly explains high variation within communities. On the other hand, species indicator values are "integrating" abiotic conditions over time. In rather stable ecosystems, their estimation can lead to a more correct habitat analysis than singular measurements of soil chemical properties. The use of quantitative instead of qualitative values led to better results, because habitat conditions in some cases differed only slightly and not enough to exclude many "non-typical" species from a community.

5.2 Habitats and plant communities

After plant communities have been initially derived from field experience and have been compared with the help of indicator values and cluster analysis, here they will be assigned to phyto-sociological units from literature, as far as possible. However, nomenclature is varying between authors, so that classification is only rough. As specific literature on Estonian plant communities was not available in English, DIERßEN (1996) was used as the main reference because of its focus on northern Europe.

Some of the plant communities found in Vöigaste can be categorised as follows:
Alvar grassland (A) – class Festuco-Brometea ("Halbtrockenrasen"). Low productivity during summer aridity, impeded mineralisation due to high pH; traditionally grazed extensively; regionally varying species pool.
Temp. wet rich fen (C) – alliance Molinion caeruleae ("Pfeifengras-Streuwiese"). Semi-natural community of unfertilised, mown fens with fluctuating groundwater table.
Perm. wet rich fen (D) – alliance Caricion lasiocarpae ("Fadenseggen-Niedermoor"). Calcareous, mesotrophic fen (peat) with high bryophyte coverage.
Hardwood forest (G) – alliance Tilio-Acerion ("Linden-Ahorn-Wald"). Dry to moist, nutrient-rich habitat.
Wet deciduous forest (H) – alliance Alnion incanae ("Erlen-Eschen-Ulmen-Wald"). Azonal vegetation on gleyed soils with high groundwater table; nitrophilous, shade- and humidity-tolerant species.
Swamp forest (J) – alliance Alnion glutinosae ("Schwarzerlen-Bruchwald"). Nitrophilous tall forbs on organic peaty soils lacking oxygen; hummocks.

The communities of semi-open habitats (E, F, K) can be regarded as intermediate or transitional. KUKK & KULL (1997) mention twelve communities characteristic to wooded meadows, but a classification of the abandoned wooded meadows in Vöigaste is not possible. DIERßEN (1996) distinguishes several ecological groups of ground vegetation in forests in a gradient of nutrients and moisture, which correspond well to the communities in the study area:
Eutrophic, medium moist (fresh): *Paris quadrifolia, Polygonatum verticillatum, Milium effusum* (corresponding to G)
Eutrophic, moist: *Filipendula ulmaria, Angelica sylvestris, Cirsium palustre, Valeriana officinalis* (corresponding to E2 and H)
Eutrophic, wet: *Salix spp*. (corresponding to J)
Mesotrophic, wet: *Caltha palustris, Potentilla palustris, Carex nigra* (corresponding to D)

In general, the plant communities described for Vöigaste Forest are in accordance with literature, as well as with the more "objective" cluster analysis although the latter considered only presence and absence of the more common species.

5.3 Diversity and succession

In nature protection management, species diversity is often a main objective, while undisturbed succession is sometimes desired, and sometimes a serious handicap. In any case, the subjects are closely related and will be treated in a common chapter here.

5.3.1 Diversity

Vöigaste Forest is a region very rich in species. It must be considered that, due to the short time of the study (June / July) and the large area, a certain number of species could not have been found and rare ones may have been overlooked. This plant (and also animal) diversity is favoured by many aspects mentioned before: the geographic location, age, area and structure of the forest, the variety of soil conditions and of micro-habitats, the proportion of dead wood, differentiated human influence, frequency of grazing animals, etc. These causes are often given in literature as well, e.g. DUMORTIER ET AL. (2002), KOUKI ET AL. (2001), JENSEN & HOFMANN (2002).

As all influences interact in any given place, it is not surprising that the only correlation of species number to a single abiotic parameter was found for moisture. From this correlation, however, it should not be concluded that drier habitats are more valuable, because many species of fens and other wet habitats are “specialists” and occur nowhere else. In the study area, many legally protected species were found only in rich fens.

Diversity can be looked upon along different spatial scales, one of which is found on wooded meadows. Some general reasons for the high species diversity on wooded meadows have already been given above (see Introduction), and are applicable for the investigated wooded meadows as well. The light gradient that was investigated exemplarily on Laelatu (Figure 6), but occurs also in other formations, causes a distribution of species according to their usual habitats, growth forms and life cycle strategies:

In spots receiving much sunlight, meadow species are found, as for example *Leontodon hispidus* (light indicator value 8), *Sesleria caerulea* (8), *Scorzonera humilis* (7), *Succisa pratensis* (7). These plants are perennials, but need to produce seeds for dispersal (GRIME ET AL. 1990). By their hemicryptophytic life form, they are adapted to the impacts by mowing or grazing, but susceptible to overgrowing if management stops. Other species are more shade-tolerant: *Convallaria majalis* (indicator value 5), *Fraxinus excelsior* (4), *Viola mirabilis* (4), *Hepatica nobilis* (4), *Melica nutans* (4), *Anemone nemorosa* (x). They are often geophytes or hemicryptophytes and can take advantage of sunlight in spring, before the tree canopy closes. Therefore, they are also more tolerant to overgrowing by tall, late developing grasses and shrubs.

Wooded meadows are ideal habitats for many animal species. Birds especially are dependent on vegetation structure and mosaic rather than on single tree species. On the other hand, oak as a common tree on wooded meadows is the main habitat and food source of numerous specialised insects (REIF ET AL. 2000). TALVI (1995) found a higher diversity of carabid beetles in wooded meadows than in neighbouring forests or meadows on Saaremaa island (western Estonia). As with plants, forest and grassland beetle species are mixed, and many rare species exist.

As a part of Matsalu Nature Reserve, Vöigaste Forest as a whole contributes to the ecosystem diversity of the area, being home to many rare animal species (e.g. black stork (*Ciconia nigra*), own observation). Due to its “wilderness”, the forest provides habitats for territory-demanding mammals (elk, wolf, bear, lynx, beaver), as well as for amphibians, reptiles and invertebrates sensitive to environmental changes.

5.3.2 Succession

When wooded meadows are abandoned, higher growing species can take over which cast shadow on the ground vegetation, spread vegetatively, or whose seeds develop later in summer (KUKK & KULL 1997). This can be recognised easily in Vöigaste (formations E1 and E2), where important species are *Brachypodium pinnatum, Calamagrostis epigeios, Aegopodium podagraria, Melampyrum nemorosum, Mercurialis perennis, Inula salicina, Filipendula ulmaria, Phragmites australis*. KUKK & KULL (1997) outline a general course of succession on old wooded meadows, which is roughly applicable to the study area:

After cessation of mowing, nutrients are not longer extracted, litter accumulates, and the ground microclimate becomes moister. Tussocks can be formed by *Molinia caerulea* and other graminoid species. The dense herb layer as well as extreme humidity or aridity of the soil can delay the growth of woody species (DIERßEN 1996), but eventually shrubs and trees will invade. Herb species of shadow habitats are favoured, and diversity decreases. When canopies close after some decades, an ash-alder-poplar forest has developed with shrubs like *Corylus avellana, Prunus padus, Frangula alnus* and *Salix spp*. underneath, and only a few old trees bear witness of the previous management. If old ditches are decaying, sites can get wetter and succession takes a different course. In a study on wooded meadows in Sweden, HANSSON & FOGELFORS (2000) found a decline in species richness after eight years (with only *Convallaria majalis, Fragaria spec*. and *Molinia caerulea* increasing), and a closed birch forest after 15 years.

These final stages resemble the “normal” deciduous forests (H) found in Vöigaste, but in most plant communities of the study area, it is not possible to determine exactly the different successional stages. Definitions of wooded meadows and times of their abandonment are largely unclear, so that succession on wooded meadows can rarely be distinguished from that in other semi-natural communities in this study.
Nevertheless, some developments can be identified:

<u>Alvars</u>: They were mostly used for grazing or haymaking (T. KALJUSTE, pers. communication) and not as wooded meadows. Alvars usually show low productivity and high species richness, comparable to calcareous grasslands (“Kalkmagerrasen”) of central Europe (DIERßEN 1996). After abandonment, aut-eutrophication occurs, rhizome-

and tussock- forming species and geophytes are favoured (KAHMAN ET AL. 2002). Together with fallow herb species (*Galium boreale, Filipendula vulgaris*), shrubs invade such as *Juniperus communis* and *Rhamnus cathartica* (DIERßEN 1996). Depending on soil depth and nutrient availability, various forest types can develop (PAAL 1998).

Fens: The growth of shrubs is often repressed in wet habitats so that fens can remain open for decades without human influence (PFADENHAUER 1997), depending on the degree of hydrological dynamics. In other cases, fens are only kept open by regular management. According to ELLENBERG (1996), abandonment is first recognisable by invading tall forbs (*Filipendula ulmaria, Lysimachia vulgaris*), or *Phragmites australis* and *Carex* species in wetter places. Woody species like *Frangula alnus, Alnus incana* and *Salix cinerea* primarily colonise the drier tussocks of *Molinia* and *Carex*. *Populus* sprouts rise out of rhizomes (ELLENBERG 1996).

In the fens in Vöigaste, often sparse stands of single *Betula* and *Populus* trees are found (plant community F). They seem to be planted, but supposedly are natural (K. LOTMAN, pers. communication). The low shrubs in-between are partly suppressed by grazing, but can develop to form very dense stands, and then the field layer diversity is diminished severely. Only when alder and birch have thinned out and grown higher, more light falls in, and a mixed deciduous forest (H) or swamp forest (J) develops. This sequence is illustrated by the relevés (53-56, 115, 116) made in plot 116.1 and 116.5 (see Differentiated table, Appendix). Due to the trees' higher transpiration, soils may also become drier in the course of succession (DIERßEN 1996).

Forest clearings: While small openings in the tree canopy do not cause significant changes in microclimate and species are similar to the surrounding forest, larger areas show characteristics of grassland. According to DIERßEN (1996), such semi-open structures can attract grazing animals (deer, elks), and their role in repressing shrub growth should be taken into account.

Depending on humidity, various shrubs can dominate (*Populus tremula, Betula pubescens, Frangula alnus, Salix spp*.). In the course of time, the fast and densely growing "pioneer" bushes of *Frangula* and *Salix* will reach their maximum height (3-5 m) and then be outgrown by *Betula, Populus* and *Fraxinus* trees, whose shade limits survival of the undergrowth. Eventually, a deciduous forest of type (H) will develop, similar to the overgrown wooded meadows. With regard to habitat diversity, forest clearings can play similar roles as wooded meadows.

Forests: The coverage of tree canopies is not complete so that there are always patches suitable for more light-demanding plants. Although some parts of Vöigaste Forest, especially swamp areas, may never have been clear-cut, human and animal influence (grazing, digging, trampling, manuring, dam-building) and the ecosystem's internal mosaic cycle have always provided a heterogeneity of habitats and a basis for species richness. Processes in openings have been explained above.

The main developments described here are in accordance with general succession theories. WHITTAKER (1975) cites the following characteristics of succession:

- increasing biomass
- increasing nutrient stock
- decreasing net productivity
- increasing height and stratal complexity
- increasing species richness (may fluctuate with interaction of strata)

Only the last point must be regarded as critical and is strongly scale-dependent, as found also by MILBERG (1995) on a grassland in Sweden. For the time prior to the domination of tall and/or woody species, their occurrence indeed often increases the total species number.

Considering these observations and interrelations, the following conclusions can be made: All parts of Vöigaste Forest are valuable habitat for plant and animal species. Especially the wooded meadow communities with high small-scale diversity, as well as some of the open wetlands, depend on continuing human management. Without this periodical disturbance, habitats will become more uniform, and species richness will decline at least on a small scale. Large-scale diversity, however, will be ensured by the natural mosaic of ecosystems and microhabitats, so that most species will continue to find their niches in Vöigaste Forest.

5.4 Protection value and restoration of habitats

Of the natural plant communities found in Vöigaste Forest, especially rich fens, swamp forests and old-growth deciduous forests are considered valuable and worth of protection by various authors (KÜLVIK ET AL. 2001, PAAL 1998, PAAL ET AL. 1998). According to PAAL (1998), 90% of all rich fens in Estonia have been subject to anthropogenic alterations in the past. Old forests feature numerous key habitats for wildlife, such as dead wood, temporal waterbodies, rocks, ant hills, stone walls (KÜLVIK ET AL. 2001). The main threat to these originally widespread habitats has been drainage for forestry and agriculture, so that it is important to protect the remaining intact areas.

While wetlands and forests are conserved mainly by not interfering with natural processes, the plant communities of semi-natural grasslands (here esp. alvars) and wooded meadows are adapted to continuous management. The following reasons are given by KUKK & KULL (1997) for protecting wooded meadows, but they are also applicable to open grassland: species diversity, scientific interest, possibility of “green” farming and eco-tourism, cultural heritage and aesthetic aspects. As extensive forms of land use are endangered by intensification as well as abandonment, efforts for their protection must include financial support and encouragement of farmers to resume management on these rather unproductive lands.

The seed bank is an important component in the re-vegetation of an area after restoration measures (e.g. cutting of shrubs), and numerous studies have been carried out on the seed bank of fallow grasslands. European calcareous grasslands are treated e.g. by POSCHLOD ET AL. (1996) and DAVIES & WAITE (1998), while MITLACHER ET AL. (2002) and KALAMEES & ZOBEL (1998) focus on wooded meadows. It has been observed that relatively few typical species of calcareous grassland form persistent soil seed banks (i.e. >20 years), and many seeds do not survive for more than 2 years. Even in intact open grassland, many field layer species are not found as seeds. Presumably their seed banks are transitional, or they depend on vegetative propagation. KUKK & KULL (1997) describe the same for wooded meadows. In traditionally managed grassland, diaspore transport by grazing animals, especially sheep, is considered an important means of dispersal.

Invading shrubs are mostly not recruited from the seed bank, but develop from suckers, runners or rhizomes (e.g. *Populus, Betula, Frangula*). Herb species that form tussocks and/or are adapted to lateral spread by stolons can survive even in old fallow sites, whereas therophytes, short-lived hemicryptophytes and rosette plants are most sensitive to overgrowing (POSCHLOD ET AL. 1996, KAHMEN ET AL. 2002). Examples for vulnerable grassland species also found in Vöigaste are *Anthyllis vulneraria, Polygala spp., Centaurea scabiosa, Cirsium acaule*. Less endangered are species of more robust life and growth forms, such as *Medicago lupulina, Helictotrichon pratense, Hypericum perforatum, Brachypodium pinnatum, Agrimonia eupatoria, Primula veris* (POSCHLOD ET AL. 1996). In the case of abandoned wooded meadows, species numbers in the field layer and the seed bank were found to drop from 52 to 18 on a scale of 4 m^2; grassland plants were substituted by forest species (MITLACHER ET AL. 2002). In a study by KALAMEES & ZOBEL (1998), only 8-10 typical grassland species survived succession in the seed bank on Laelatu wooded meadow.

The authors generally agree that the seed bank can only play a very limited role in the restoration of species-rich calcareous grassland and wooded meadows so that seeds should be provided from neighbouring grassland by hay dispersal or animal movement. KIEFER & POSCHLOD (1996) attempted a restoration of calcareous grassland by clear-cutting after 20 years and found that regeneration in the beginning was mainly from the seed bank. Ruderals of the first years were soon replaced by more typical grassland species (hemicryptophytes). After 5 years, 59% of the species of adjacent grassland had established in the plots. PÄRTEL ET AL. (1999) investigated grassland in Hanila (Läänemaa) and state that 40-50 years are needed for its restoration (similar: ZOBEL ET AL. 1996). For restoration plans, the possibilities for animal re-colonisation of structurally and floristically restored habitats must also be taken into account.

As restoration is thus difficult and expensive, priority must be given to conservation of areas still intact. Many studies have been conducted to find the best and easiest management methods, mostly with the aim to maintain open landscapes and species diversity. There are four main methods discussed in nature conservation to restrict growth of woody species:

Mowing is generally considered best for balancing the competition between species, but is also the most expensive, especially if done by hand (e.g. on wet, uneven ground or in wooded meadows). Mowing every third year can inhibit shrub growth (HANSSON & FOGELFORS 2000), but for conservation of high species diversity, yearly and late mowing is necessary in most plant communities.

Mulching (leaving litter on the ground after mowing) has similar effects as mowing, but a dense litter layer can repress small, delicate plants by casting shadow. Microclimate on the soil surface is cooler and moister, and in wet habitats microbial activity is too low to ensure decomposition (PFADENHAUER 1997).

Grazing leads to a more selective removal or "cutting" of plants; several species are not eaten at all (*Juniperus communis, Cirsium spp*.), others are not palatable to all grazing animals. According to HAEGGSTRÖM (1990), sheep in general graze more selectively than cattle, eating more tall herbs and woody plants and less graminoids than cows. Effects of grazing are not only removal and defoliation of plants, but also trampling, manuring and seed dispersal, which may or may not be desired. Grazing leads to more spatial variation than mowing. Despite the theoretical advantages of mowing, KAHMEN ET AL. (2002) found no difference in species composition between mown, grazed and mulched grassland plots after 25 years (experiment initiated by K.-F. Schreiber).

Burning is no traditional method of grassland management (in northern and central Europe), and effects are mostly undesired. Species composition of the plant community is changed (e.g. geophytes are favoured) so that it cannot be recommended for conservation purposes (KAHMEN ET AL. 2002).

On wooded meadows, combining mowing and grazing has a long tradition, but discussion is continuing if this is necessary, neutral or harmful. Grazing does certainly not suffice to conserve wooded meadows and should not be too intense; mixed grazing of sheep and cattle may be ideal, also from an economical point of view (HANSSON & FOGELFORS 2000, HAEGGSTRÖM 1990, PAAL 1998). The management aspects discussed here are valid only for managed grasslands and wooded meadows; in wetter habitats (e.g. fens) overgrowing is slowed considerably and includes different species. Mowing frequency has to be adjusted.

The essential statements of this literature overview are for Vöigaste:
All plant communities are worth of protection, which should include active management inputs in the case of alvar grasslands, wooded meadows and (partly) fens. Furthermore, the whole area as a non-fragmented, diverse and well-structured landscape is a valuable component of Matsalu Nature Reserve. It merits administrative, scientific and public attention not only for its remnants of wooded meadows, but as a unique, complex woodland developing its internal mosaic of habitats, plant communities and successional stages.

6 Conclusions and Management Suggestions

In this final chapter, the information gained during the study and discussed above will be employed to assess the possible development and management of Vöigaste Forest.

As part of Matsalu Nature Reserve, Vöigaste is protected from most agricultural and forestry activities. At the moment, it serves primarily as undisturbed habitat for flora and fauna, but it includes valuable semi-natural areas and is also suitable for research on landscape dynamics and different land use methods. Therefore, it is suggested that the wetland and forest areas be mostly left to their natural development (which may be one-directional, cyclic or stochastic), being valuable communities even on a larger scale. In drier habitats, the previous management should in parts be resumed, but conservation must have priority over restoration. Taking advantage of the large area, a variety of strategies and methods can be tested in order to gain knowledge applicable to similar landscapes in the region. All management should be extensive and leave space and time for habitat diversity on all scales. These efforts would certainly merit extra financial support. Suggestions are in detail:

- Conservation of wooded meadows where the structure is still intact and access easy. Within the study area, plots 111.7, 112.2, 117.1 (forest map) are the most promising. Different regimes of mowing and/or grazing can be applied.
- Conservation of accessible grasslands by mowing and/or grazing; leaving others to succession.
- Conservation of open fens by mowing where necessary to prevent overgrowing by reed or shrubs.
- Setting up permanent plots within the managed plots as well as others, to monitor changes in plant community structure in the course of succession.
- Experimenting with other forms of land use, e.g. forest pasture or selective cutting of forest trees (both increasing habitat diversity).
- Making part of the forest accessible to the public (education, tourism) by installation of nature trails, information boards etc.
- Conducting further research and monitoring, e.g. on seed banks, soils, water regime and the fauna. Results can be integrated in regional and national inventories and databases.

However, in following these suggestions or other management plans, priority must be given to the area’s significance as natural and cultural heritage. This is not restricted to wooded meadows or bird habitats, as is the present focus of Matsalu Nature Reserve. Many plant communities in Vöigaste Forest are valuable in the regional, national and international context.

7 Summary

The aim of this study was to characterise the habitats, plant communities and successions occurring in Vöigaste Forest, and to give management suggestions for this part of Matsalu Nature Reserve. The study area encompasses 700 ha of hemi-boreal deciduous forest, semi-open woodland, fens and grassland. It is situated in the south-western part of the nature reserve, in western Estonia, on calcareous and partly gleyic soils. The climate is atlantic-continental.

Most of the land had been used for agriculture and forestry in earlier times. Part of the area had originally been managed as wooded meadows, a traditionally widespread vegetation type of northern Europe. Today, wooded meadows are of close interest for nature conservationists because of their extraordinary small-scale species richness, which is only made possible by the regular disturbance of continuous, extensive management.

For analysis of vegetation and habitats (June/July 2002), basic field methods were used: vegetation relevés after Braun-Blanquet, rough soil analysis, light measurements (potential hours of sunshine). For classification and comparison of plant communities, Ellenberg indicator values for the field layer species were calculated, and a cluster analysis was carried out. Different parameters were correlated and illustrated in diagrams, in order to clarify interactions. It was possible to distinguish the following plant communities, which differ in structure, species composition and indicator values:

A: Alvar grassland
B: Moist grassland
C: Temporarily wet rich fen
D: Permanently wet rich fen
E: Abandoned (but structurally distinguishable) wooded meadow, dry and wet variant
F: Temporarily wet rich fen, overgrowing
G: Hardwood forest
H: Wet deciduous forest
J: Swamp forest
K: Intact wooded meadow, outside Vöigaste Forest (Allika, Laelatu)

Altogether, 335 species of vascular plants were identified in the study area, which is half the number occurring in Matsalu Nature Reserve. Among them were 13 species protected in Estonia (categories II and III), mainly *Orchidaceae*. Species richness was highest (as expected) in the intact wooded meadows, but several protected species were found only in rich fens. Nevertheless, all communities have to be considered valuable, offering numerous microhabitats and niches for plant and animal species.

Being part of the nature reserve, there is no management done in Vöigaste Forest at the moment, and succession is only (partly) inhibited by browsing wild animals (deer, elks). As no intact wooded meadows remain in Vöigaste Forest and the time of their abandonment is mostly unknown, it is only possible to draw some rough conclusions on the succession in these habitats. Grassland and old wooded meadows become overgrown with tall forbs, grasses and bushes, the species depending on the soil properties. After some years, a few species dominate, and diversity declines. However, the decline is in this case true only for small-scale richness, since the overall spatial and temporal diversity of environments in this area (moist and dry, light and shadow) provides habitat for species of very different requirements. The „wild“, old and richly structured woodlands are valuable also for a variety of mammals, reptiles, amphibians and invertebrates.

Management should give priority to keeping open rich fens (as endangered habitat type in Estonia) and, if possible, wooded meadows and alvars. Otherwise, forest and wetlands should be left to follow their „internal mosaic cycle“ of successional stages. Restoration of grassland or wooded meadows on overgrown sites is costly and not promising, especially because new seeds would have to be brought in. Instead, different management methods of mowing, grazing etc. could be applied and evaluated for future conservation plans in the region. Scientific monitoring of successions and management impacts is desirable, and the area could be integrated into Matsalu's nature-tourism concept. All management and interventions should be extensive and leave space and time for habitat diversity on all scales.

8 Zusammenfassung

Ziel der Arbeit war es, die Standorte, Pflanzengesellschaften und Sukzessionen im Vöigaste Wald zu beschreiben und Vorschläge zur Bewirtschaftung in diesem Teil des Naturschutzgebietes Matsalu zu machen. Das Untersuchungsgebiet umfaßt 700 ha hemiborealen Laubwald, halboffene Waldgebiete, Niedermoore und Grasland. Es liegt im südwestlichen Teil des Naturschutzgebietes, im Westen Estlands, auf carbonatreichen und z.T. vergleyten Böden. Das Klima ist atlantisch-kontinental.

Das Gebiet wurde früher landwirtschaftlich und forstlich genutzt, teilweise als Gehölzwiesen (engl. wooded meadows, estn. puisniidud). Hierbei handelt es sich um eine ehemals weit verbreitete Landnutzungsform in Nordeuropa. Heute sind Gehölzwiesen von großem Interesse im Naturschutz, da sie eine außergewöhnliche kleinräumige Artenvielfalt aufweisen, die nur durch die regelmäßigen Störungen einer kontinuierlichen, extensiven Nutzung erhalten wird.

Für die Charakterisierung von Vegetation und Standorten wurden grundlegende Feldmethoden angewandt (Juni / Juli 2002): Vegetationsaufnahmen nach Braun-Blanquet, grobe Bodenansprachen, Horizontoskop-Lichtmessungen (potentielle Sonnenstunden). Um die Pflanzengesellschaften zu klassifizieren und zu vergleichen, wurden die ökologischen Zeigerwerte nach Ellenberg berechnet sowie eine Ähnlichkeits-Cluster-Analyse der Aufnahmen durchgeführt. Um Zusammenhänge zu verdeutlichen, wurden verschiedenen Parameter verglichen und graphisch dargestellt.
Die folgenden Pflanzengesellschaften konnten nach Struktur, Artzusammensetzung und Zeigerwerten unterschieden werden:

A: Alvar-Grasland (Halbtrockenrasen)
B: Frisches Grasland
C: Zeitweise nasses Niedermoor (Pfeifengras-Streuwiese)
D: Ständig nasses Niedermoor (Fadenseggen-Niedermoor)
E: Aufgelassene (aber noch in der Struktur erkennbare) Gehölzwiese; trockene und nasse Variante
F: Zeitweise nasses, verbuschendes Niedermoor
G: Edellaubwald (Linden-Ahorn-Wald)
H: Nasser Laubwald (Erlen-Eschen-Ulmen-Wald)
J: Erlenbruchwald
K: Erhaltene Gehölzwiese, außerhalb von Vöigaste (Allika, Laelatu)

Insgesamt wurden 335 Arten von Gefäßpflanzen im Untersuchungsgebiet gefunden, d.h. die Hälfte aller in Matsalu vorkommenden. Von diesen sind 13, v.a. *Orchidaceae*, in Estland gesetzlich geschützt (Kategorien II und III). Die höchsten Artzahlen wiesen, wie erwartet, die erhaltenen Gehölzwiesen auf, während einige der geschützten Arten nur in Niedermooren vorkamen. Trotzdem sind alle Pflanzengesellschaften als wertvoll zu betrachten, da sie zahlreiche Kleinstandorte und Nischen für Tier- und Pflanzenarten bieten.

Momentan erfolgen kaum Eingriffe im Vöigaste Wald, so daß Sukzessionsfolgen höchstens durch Wildverbiß (Rehe, Elche) verzögert werden. Da die Gehölzwiesen im Vöigaste Wald jeweils zu unbekannten Zeitpunkten brachgefallen sind, kann man die Sukzessionsverläufe auf diesen Standorten nur grob skizzieren. Wenn Grünland und Gehölzwiesen verbrachen, kommen zunächst Hochstauden und hohe Gräser sowie Büsche auf; welche das sind, ist standortabhängig. Nach einigen Jahren dominieren wenige Arten den Bestand, und die Gesamt-Artenzahl sinkt. Im hier betrachteten Fall ist der Effekt aber nur im kleinen Maßstab zu erwarten, da die räumliche und zeitliche Standortvielfalt (naß und trocken, hell und dunkel) für Arten mit sehr verschiedenen Ansprüchen Lebensraum bietet. Die "wilden", alten und reich strukturierten Waldgebiete sind auch wertvoll für viele Säugetiere, Reptilien, Amphibien und Wirbellose.

Das Naturschutz-Management sollte zunächst darauf abzielen, die Niedermoore als gefährdeten Standorttyp Estlands sowie möglicherweise die Gehölzwiesen und die Halbtrockenrasen offenzuhalten. Andere Feuchtgebiete und der Wald sollten der natürlichen Sukzession und damit ihrem eigenen Mosaik-Zyklus überlassen werden. Eine Wiederherstellung von weitgehend verbuschten Halbtrockenrasen oder Gehölzwiesen ist aufwendig und wenig aussichtsreich, da unter anderem neue Samen bzw. Diasporen eingebracht werden müßten. Statt dessen könnten verschiedene Bewirtschaftungsvarianten (Weide, Mahd, etc.) angewandt und hinsichtlich zukünftiger Schutzkonzepte in der Region bewertet werden. Eine wissenschaftliche Beobachtung der Sukzessionen und der Veränderungen durch Eingriffe ist wünschenswert, ebenso wie die Einbindung des Gebiets in das natur-touristische Konzept des Naturschutzzentrums. Jede Bewirtschaftung und jeder Eingriff sollte nicht zu intensiv sein und weiterhin Standortvielfalt in Raum und Zeit ermöglichen.

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10 Appendix

This appendix includes:

- Species list of vascular plants of Vöigaste Forest
- UTM co-ordinates of all relevés
- Vöigaste Forest map (with legend and translation)
- Table of average parameters of relevés used for diagrams
- Photos from Vöigaste Forest
- Differentiated table with all information of relevés (folded extra sheet)

Species list Võigaste Forest

(*= species only found by R. Böcker in April 2002)

Acer platanoides
Achillea millefolium
Achillea ptarmica
Actaea spicata
Adoxa moschatellina
Aegopodium podagraria
Agrimonia eupatoria
Agrostis cf. canina
Agrostis capillaris
Agrostis stolonifera
Alchemilla vulgaris agg.
Alisma plantago-aquatica
Allium oleraceum
Alnus glutinosa
Alnus incana
Alopecurus pratensis
Anemone nemorosa
Anemone ranunculoides
Anemone sylvestris
Angelica archangelica *
Angelica sylvestris
Antennaria dioica
Anthoxanthum odoratum
Anthriscus sylvestris
Anthyllis vulneraria
Arabis glabra
Arabis hirsuta
Arctium lappa
Arctium minus
Asperula tinctoria
Astragalus danicus
Astragalus glycyphyllos
Berberis vulgaris
Betula pendula
Betula pubescens
Brachypodium pinnatum
Brachypodium sylvaticum
Briza media
Calamagrostis canescens
Calamagrostis epigejos
Calamagrostis stricta
Calamintha acinos
Calamintha clinopodium
Caltha palustris
Campanula glomerata
Campanula patula
Campanula persicifolia
Campanula rapunculoides
Campanula rotundifolia
Campanula trachelium
Capsella bursa-pastoris
Cardamine pratensis
cf. Carduus crispus

Carex acuta *
Carex acutiformis
Carex cespitosa
Carex davalliana

Carex diandra
Carex digitata *
Carex disticha
Carex echinata
Carex elata
Carex flacca
Carex flava
Carex hartmanii
Carex hirta
Carex hostiana
Carex lasiocarpa
Carex nigra
Carex ornithopoda
Carex ovalis
Carex pallescens
Carex panicea
Carex riparia
Carex rostrata
Carex spicata
Carex sylvatica
Carex tomentosa
Carex vesicaria
Carex vulpina
Carum carvi
Centaurea jacea
Centaurea scabiosa
Cerastium fontanum
Chelidonium majus *
Chrysanthemum leucanthemum
Cichorium intybus
Cirsium acaule
Cirsium arvense
Cirsium heterophyllum
Cirsium oleraceum
Cirsium palustre
Convallaria majalis
Convolvulus arvensis
Cornus sanguinea
Corydalis solida *
Corylus avellana
Crataegus monogyna
Crataegus rhipidophylla
Crepis biennis
Crepis paludosa
Crepis praemorsa
Cypripedium calceolus
Dactylis glomerata
Dactylorhiza fuchsii
Dactylorhiza incarnata

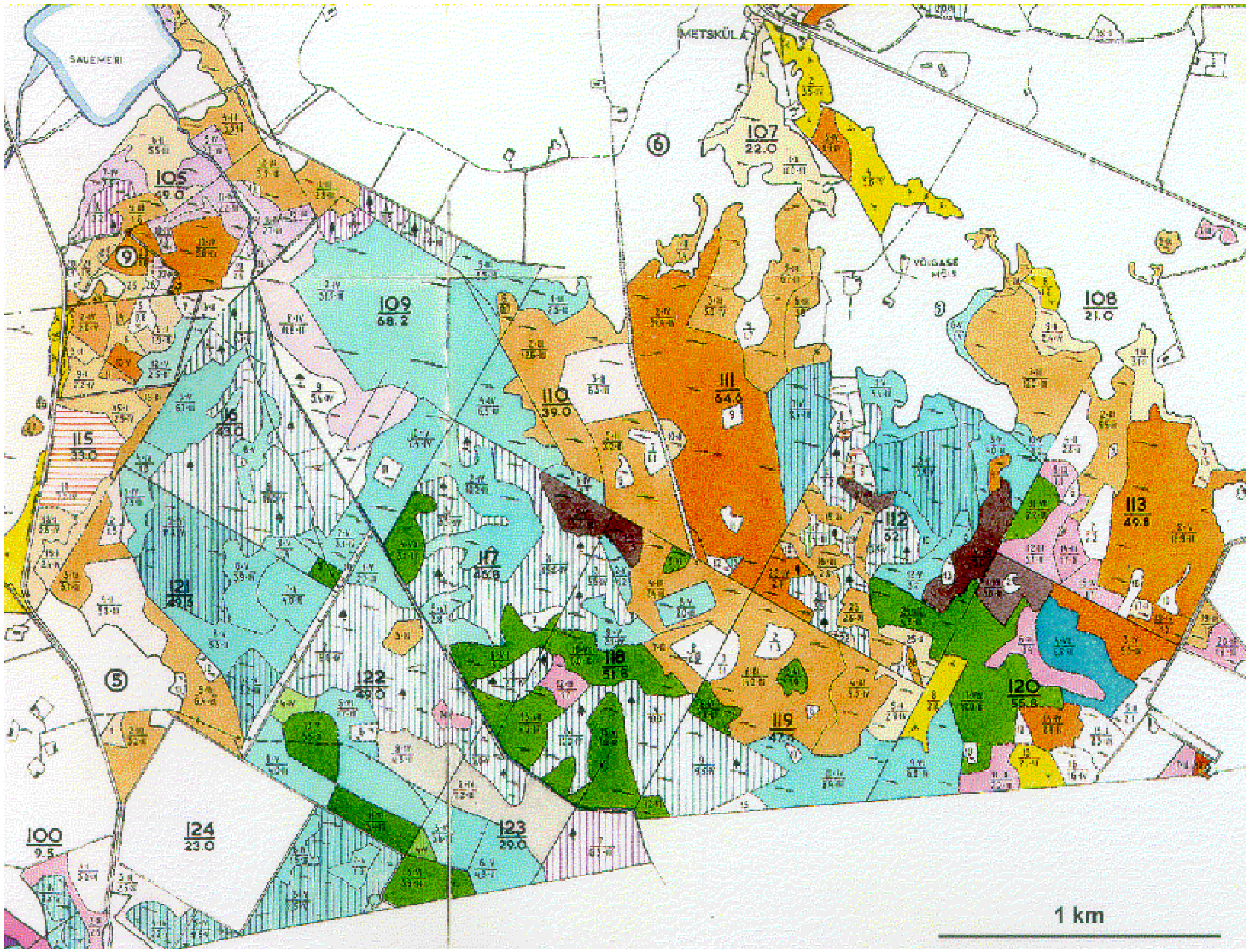
Dactylorhiza maculata
Daphne mezereum
Deschampsia cespitosa
Dianthus deltoides
Dryopteris carthusiana
Dryopteris filix-mas
Echium vulgare
Eleocharis cf. palustris
Elymus caninus
Elymus repens
Epilobium hirsutum
Epilobium palustre
Epipactis palustris
Equisetum arvense
Equisetum fluviatile
Equisetum palustre
Equisetum pratense
Equisetum sylvaticum
Eriophorum angustifolium
Eriophorum latifolium
Euphorbia palustris
Festuca arundinacea
Festuca gigantea
Festuca rubra
Festuca ovina
Filipendula ulmaria
Filipendula vulgaris
Fragaria vesca
Fragaria viridis
Frangula alnus
Fraxinus excelsior
Fumaria officinalis
Gagea lutea *
Galeopsis cf. bifida
Galium boreale
Galium mollugo
Galium palustre
Galium uliginosum
Galium verum
Geranium pratense
Geranium robertianum
Geranium sanguineum
Geum rivale
Geum urbanum
Gladiolus imbricatus
Glyceria fluitans
Gymnadenia conopsea
Helictotrichon pratense
Helictotrichon pubescens
Hepatica nobilis
Heracleum sosnowskyi *
Heracleum sphondylium
Hieracium lactucella
Hieracium pilosella
Hieracium piloselloides
Hierochloe odorata
Humulus lupulus
Hypericum hirsutum
Hypericum maculatum
Hypericum perforatum
Inula salicina
Iris pseudacorus
Juncus cf. articulatus

Juncus conglomeratus
Juncus effusus
Juncus nodulosus
Juniperus communis
Knautia arvensis
Lapsana communis
Laserpitium latifolium
Lathraea squamaria *
Lathyrus palustris
Lathyrus pratensis
Lathyrus vernus
Leontodon hispidus
Linum catharticum
Listera ovata
Lotus corniculatus
Luzula campestris
Luzula pilosa
Lychnis flos-cuculi
Lychnis viscaria
Lycopus europaeus
Lysimachia thyrsiflora
Lysimachia vulgaris
Lythrum salicaria
Maianthemum bifolium
Malus spec.
Medicago lupulina
Melampyrum nemorosum
Melampyrum pratense
Melamyrum cristatum
Melica nutans
Melilotus altissimus
Mentha aquatica
Mentha cf. arvensis
Menyanthes trifoliata
Mercurialis perennis
Milium effusum
Moehringia trinervia
Molinia caerulea
Monotropa hypopitys *
Myosotis palustris
Ononis spinosa
Orchis mascula
Orchis militaris
Origanum vulgare
Oxalis acetosella
Paris quadrifolia
Parnassia palustris
Peucedanum palustre
Phleum pratense
Phragmites australis
Picea abies
Pimpinella saxifraga
Pinguicula vulgaris
Pinus sylvestris
Plantago lanceolata
Plantago major
Plantago media
Platanthera bifolia
Platanthera chlorantha
Poa compressa
Poa nemoralis
Poa palustris
Poa pratensis
Poa trivialis
Polygala amarella
Polygala cf. comosa
Polygonatum multiflorum
Polygonatum odoratum
Populus tremula
Potentilla anserina
Potentilla erecta
Potentilla palustris
Potentilla reptans
Primula farinosa
Primula veris
Prunella vulgaris
Prunus padus
Pulmonaria obscura
Pyrola rotundifolia
Quercus robur
Ranunculus acris
Ranunculus auricomus
Ranunculus cassubicus
Ranunculus flammula
Ranunculus polyanthemos
Ranunculus repens
Rhamnus cathartica
Ribes alpinum
Ribes nigrum
Ribes rubrum
Ribes uva-crispa
Rosa spec.
Rubus caesius
Rubus idaeus
Rubus saxatilis
Rumex acetosa
Salix bicolor
Salix caprea
Salix cinerea
Salix myrsinifolia
Salix pentandra
Salix repens
Salix starkeana
Schoenus ferrugineus
Scirpus sylvaticus
Scorzonera humilis
Scrophularia nodosa
Scutellaria galericulata
Sedum acre
Selinum carvifolia
Selinum venosum
Senecio jacobaea
Senecio paludosus
Senecio sylvaticus
Sesleria caerulea
Silene dioica
Silene vulgaris
Solanum dulcamara
Sonchus arvensis
Sorbus aucuparia
Sparganium emersum
Stachys palustris
Stachys sylvatica
Stellaria graminea
Stellaria holostea
Succisa pratensis
Taraxacum officinale
Thalictrum flavum
Thalictrum cf. minus
Thalictrum simplex
Thelypteris palustris
Thymus serpyllum
Tilia cordata
Tilia platyphyllos
Torilis japonica
Tragopogon pratensis
Trifolium medium
Trifolium montanum
Trifolium pratense
Trifolium repens
Triglochin palustre
Trollius europaeus
Tussilago farfara
Typha angustifolia
Typha latifolia *
Typhoides arundinacea
Ulmus glabra
Urtica dioica
Vaccinium myrtillus
Vaccinium uliginosum
Valeriana officinalis
Valerianella locusta
Verbascum nigrum
Veronica chamaedrys
Veronica officinalis
Veronica teucrium
Viburnum opulus
Vicia cracca
Vicia sepium
Vicia sylvatica
Viola canina
Viola collina
Viola elatior
Viola mirabilis
Viola riviniana
Viola uliginosa

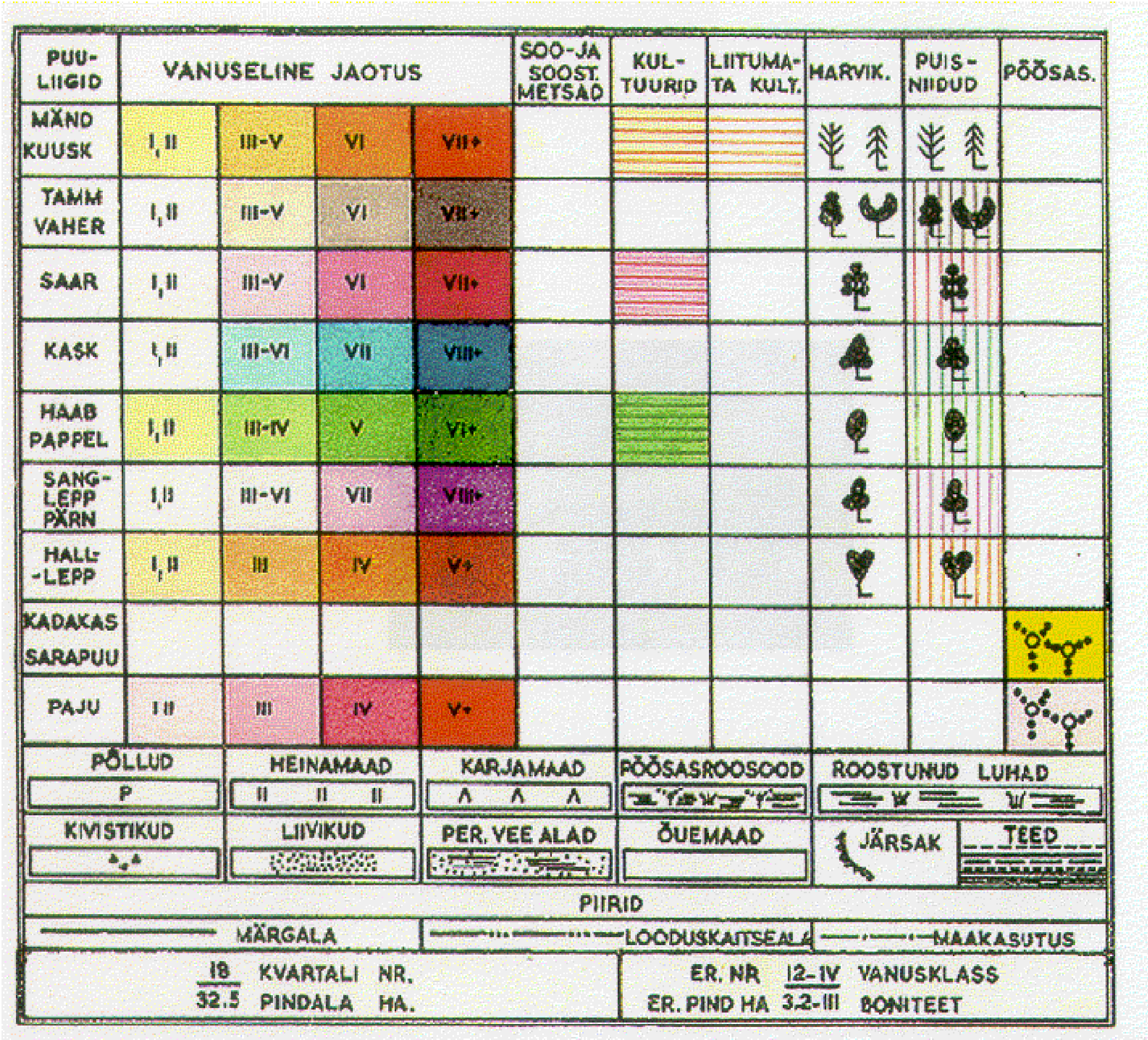
UTM Co-ordinates of Relevés

Relevé	UTM value Horizontal	UTM value Vertical
1	0650174	6509881
2	0650369	6510199
3	0654019	6510702
4	0654142	6510122
5	0653815	6510224
6	0653715	6510224
7	0653695	6510396
8	0653705	6510436
9	0653728	6510934
11	0653659	6509202
12	0653830	6509345
13	0653796	6509411
14	0652551	6511265
15	0652630	6510542
16	0652902	6510606
17	0651076	6511297
18	0652706	6510611
19	0652927	6510309
20	---	---
21	0653167	65101391
22	0652882	6510452
23	0652933	6510378
24	0653082	6510510
26	0650556	6510708
27	---	---
28	0650583	6510303
30	0650348	6510066
31	0652863	6511445
32	0650901	6511012
33	0651030	6511147
34	0651171	6511228
35	0651237	6511185
37	0651991	6510048
38	0651883	6510059
39	0651677	6510292
40	0651948	6510150
41	0652073	6509945
42	0651576	6509769
43	---	---
44	0652842	6509920
45	0652817	6510196
46	0652903	6510348
47	0653120	6510114
48	0650123	6511195
49	0651703	6509534
50	0651494	6509888
51	0651602	6509909
52	0651811	6510129
53	0650605	6510243
54	0650714	6510200
55	0650763	6510025
56	0650728	6510554
57	0650870	6510623
58	0651898	6509300
59	0652019	6509268
60	0651973	6509304
61	0651956	6509455
62	0652308	6509567
63	0652408	6509722
64	0652506	6509796
65	0652992	6510840
66	0652915	6510771
67	652708	6510742
68	0652708	6510642
69	0652703	6510382
70	0652770	6510471
71	0652433	6510100
72	0652480	6509742
73	0652308	6509351
74	0652376	6509157
75	0652485	6509390
76	0652368	6509482
77	0652436	6509594
78	0652000	6509013
79	0652080	6509089
80	0652105	6509110
81	0650844	6509394
82	0651032	6509489
83	0651163	6509525
84	0651364	6509616
85	0652071	6510362
86	0651507	6509581
87	0651483	6509668
88	0651307	6509778
89	0651466	6510189
90	0650830	6511376
91	0651155	6511204
92	0651239	6511193
93	0651027	6511155
94	0650550	6509807
95	0650540	6509958
96	0650661	6510150
97	0652579	6509775
98	0652653	6509773
99	0652823	6509934
100	0652777	6509840
101	0652408	6509772
102	0652214	6510416
103	0652909	6510584
104	0652843	6510595
105	0652900	6510671
106	0651950	6511098
107	0652187	6510475
108	0652062	6510349
109	0651868	6510021
110	0653205	6510305
111	0650670	6511223
112	---	---
113	0650898	6510568
114	0651052	6510362
115	0650867	6510551
116	0650847	6510625
T 1	0652742	6510480
T 2	0653329	6510440
T 3	---	---

Forest Map Vöigaste



Legend of forest map



Translation of relevant information:

Puuligid: Tree species
Mänd, Kuusk: *Pinus, Picea*
Tamm, Vaher: *Quercus, Acer*
Saar: *Fraxinus*
Kask: *Betula*
Haab pappel: *Populus*
Sanglepp, Pärn: *Alnus glutinosa, Tilia*
Hallepp: *Alnus incana*
Kadakas, Sarapuu: *Juniperus, Corylus*
Paju: *Salix*

Vanuseline jaotus: Groups by age
Soo- ja soost. metsad: Swamp and swampy forests
Kultuurid: Planted
Marvik: Open
Puisniidud: Wooded meadows
Pöösas: Shrub
Teed: Roads

Kvartali Nr.: Plot
Pindala ha: Area (ha)
Vanusklass: Age class
Boniteet: Quality

Table of average parameters of relevés used for diagrams

Plant community	**Average values**					
	Nitrogen	**Light**	**Reaction**	**Moisture**	**Species number**	**Pot. hours of sunshine**
Alvar grassland	2,8	7,2	7,6	5,0	32,3	1884,8
Moist grassland	4,4	6,9	6,9	5,7	38,7	1659,0
Temporarily wet rich fen	3,3	7,2	6,6	8,2	25,4	1850,7
Pmt. wet rich fen	3,8	7,5	4,7	8,2	16,9	2102,6
Aband. wooded meadow, dry	4,7	5,9	7,0	4,9	41,9	579,7
Aband. wooded meadow, wet	4,7	6,2	6,5	6,3	34,2	326,4
Rich fen overgrown	3,9	6,8	6,3	7,4	29,7	1070,3
Intact wooded meadow	3,7	6,4	6,8	5,4	61,0	534,5
Hardwood forest	4,9	4,5	7,0	4,6	30,7	197,2
Wet deciduous forest	5,2	5,8	6,9	6,8	27,5	285,8
Swamp forest	4,9	6,5	6,8	8,3	21,5	196,6