The forests of the North-Estonian Klint; the north-easternmost representatives of the EU Habitat Directive *Tilio–Acerion* forests of slopes, screes and ravines

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Forests growing on talus slopes of the North-Estonian Klint were studied. According to the soil-cover properties, the studied sites of the klint can be divided into six soil complexes. Eleven vegetation types were established: (1) *Ulmus glabra–Fraxinus excelsior–Aegopodium podagraria*, (2) *Ulmus glabra–Alnus incana–Matteuccia struthiopteris*, (3) *Tilia cordata–Hepatica nobilis–Actea spicata*, (4) *Ulmus glabra–Acer platanoides–Allium ursinum*, (5) *Ulmus glabra–Mercurialis perennis*, (6) *Ulmus glabra–Brachythecium rutabulum–Thuidium philibertii*, (7) *Alnus glutinosa–Athyrium filix-femina–Impatiens noli-tangere*, (8) *Alnus incana–Urtica dioica–Dryopteris expansa*, (9) *Tilia cordata–Picea abies–Oxalis acetosella–Eurhynchium angustirete*, (10) *Ulmus glabra–Alnus glutinosa–Lunaria rediviva*, and (11) *Alnus glutinosa–Tilia cordata–Impatiens parviflora*. The first type embraces the largest number of communities and is presented along the klint in many sites. The soil variables affecting vegetation variation most, are the specific surface area and strongly correlated with it, the nitrogen and carbon content. The Estonian klint forests have rather good affinity with south Scandinavian respective stands growing on slopes or screes on calcareous base rich soils. Certain similarity can be followed also with central European communities of *Fraxino–Aceretum*, *Acero–Tilietum* and *Alno–Fraxinetum* associations.

Key words: limestone escarpment, eutrophic forests, *Lunaria rediviva*, Natura 2000, Rendzic Leptosols, soil complexes.

Introduction

Along the southern shore of the Gulf of Finland stretches a long and magnificent limestone escarpment, the North-Estonian Klint, forming a part of the Baltic Klint. The latter extends from Öland in the west (southwest) to Lake Ladoga in the east (northeast). The height of the North-Estonian Klint varies, ascending generally from west to east and reaching the maximum relative height of 56 m at Ontika (Raukas 1996); after that it gradually descends again. In many places the klint falls steeply into the sea, but more often the coastal plain of various widths (up to

6 km) remains between the escarpment foot and the sea. The klint forms an important exposed geographical boundary in northern Europe: it is situated on the border of crystalline rocks of the Fennoscandian Shield and sedimentary rocks of the East-European Platform (Tammekann 1940, Miidel 1997). The geological section of the North-Estonian Klint is rather simple: the Cambrian and Ordovician clays, silts, argillites and sandstones cropping out in its lower part are overlain by Ordovician limestones and dolomites (Miidel 1997). In addition to the North-Estonian Klint, numerous bedrock scarps are to be found in the western central part of the Estonian mainland and on the northern coasts of the islands of Saaremaa and Muhu, representing the West-Estonian (Silurian) Klint (Aaloe & Miidel 1967).
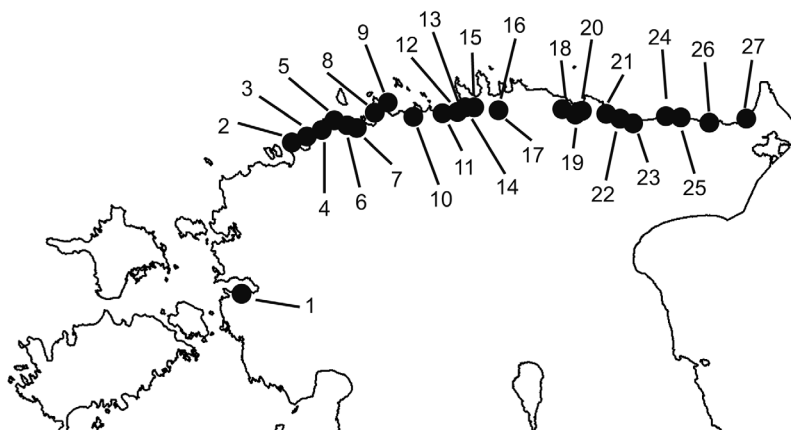
The foot of the escarpment constitutes usually a talus slope (scree), made of limestone or sandstone blocks partly covered with finer weathered material, clay or primitive soil which is amply inundated with calcareous and nutrient-rich seeping ground water or springs. Closeness to the sea and being sheltered from the escarpment, creates a unique microclimate, which supports a diverse flora, exceptional to Nordic biota (Ingerpuu *et al*. 2001, Paal *et al*. 2001). Ecological conditions similar to the klint talus slopes can be found also in the canyon-like valleys of some north Estonian rivers (especially Valgejõgi near Nõmmeveski).

The first floristic notes concerning klint forests were published in the second half of the 19th century by Schmidt (1859). Gruner (1864) gave a short characterization of habitat conditions of these forests, pointing out that (i) below the shallow humus horizon lay easily wheathering rocks, (ii) here the closeness to the sea has a great importance, (iii) the habitats have a northern exposition and, (iv) the habitats have a stable water supply. Rather voluminous descriptions of klint forests flora and habitats can be found in the papers of Russow (1864, 1889). Taking into account the peculiarities of klint forests features, Lippmaa (1935) differentiated the North-Estonian Klint area to a separate plant geographical subregion — *Estonia clivosa*. In the recent classification of the Estonian vegetation site types (Paal 1997) the klint forests constitute a separate *Lunaria* forest site type in the type group of eutrophic boreo-nemoral forests.

Due to the fact that during the Soviet time the main part of the klint belonged to the state border zone where any movement of people was very restricted and in many places totally prohibited, these forests were more thoroughly studied only within the borders of the Lahemaa National Park (Kalda 1988). For other localities they were described rather briefly only in the frames of a larger overview of Estonian nemoral forests (Kalda 1958, 1960, 1962, Laasimer 1965). Masing (1966) was the first who classified these forests into a separate klint forest site type. Nevertheless, in the official Estonian forests site type classification (Lõhmus 2004) used for forests taxation the klint forests are not recognised. This is perhaps due to the scarcity of relevant data, but also due to the restricted area and the small economic importance of these forests in comparison with forests of other site types covering large areas. Still all klint forests are evaluated in Estonia as rare and threatened (Paal 1998) and in the last decade they have evoked again great attention in connection with the Natura 2000 project (Paal 2007). According to the EU Habitat Directive criteria (EC 1992), these forests belong to the type 9180 '*Tilio–Acerion* forests of slopes, screes and ravines', having in the context of biodiversity protection the priority rank for all Europe. The Estonian klint forests represent the north-easternmost variety of the concerned type.

Besides their ecological conditions, the klint forests are remarkable at least due to two other facts. First, Estonia is situated almost in the northern distribution limit of deciduous forests (cf. Kalela 1954, Jalas 1957, Laasimer 1962, 1965, Hinneri 1972). The study of marginal phenomena has always been a challenge to scientists because they may contain important information for comparison and also for explanation of the nature and development of many typical or ordinal objects. Second, most of the Estonian recent deciduous forests have been formed as secondary stands from mixed spruce forests after selective cutting of spruce, or from mixed pine-oak forests after considerable removing of pine. Primary deciduous forests are to be found only on the slopes of limestone escarpment, and probably on slopes of some ancient valleys (Kalda 1962) where their management has been too

Fig. 1. Location of the sample areas. Notations W and E in the end of area names mean that the area was divided into two parts according to their quarter and analysed independently.

No.	Sample area	Lat. N	Long. E	No.	Sample area	Lat. N	Long. E
1	Salevere	58°41.48′	23°35.37′	15	Kolga N	59°30.57′	25°36.75′
2	Leetse	59°22.10′	24°07.87′	16	Nõmmeveski W	59°30.50′	25°47.54′
3	Laulasmaa	59°23.92′	24°15.08′	17	Nõmmeveski E	59°30.59′	25°47.55′
4	Türisalu	59°25.03′	24°18.94′	18	Kunda W	59°30.96′	26°29.30′
5	Suurupi	59°27.63′	24°22.54′	19	Kunda E	59°30.63′	26°30.13′
6	Muraste	59°27.46′	24°28.69′	20	Lontova	59°30.58′	26°33.79′
7	Rannamõisa	59°26.59′	24°31.42′	21	Kalvi	59°28.80′	26°48.79′
8	Viimsi W	59°30.98′	24°50.35′	22	Aseri	59°26.73′	26°54.35′
9	Viimsi E	59°30.14′	24°52.38′	23	Purtse	59°26.04′	27°01.37′
10	Ülgase	59°29.37′	25°05.37′	24	Saka	59°26.44′	27°12.79′
11	Valkla	59°29.40′	25°18.53′	25	Ontika	59°26.66′	27°19.18′
12	Tsitre	59°30.58′	25°29.49′	26	Toila	59°25.99′	27°28.17′
13	Muuksi	59°30.73′	25°31.84′	27	Meriküla	59°24.49′	27°56.41′
14	Kolga W	59°30.25′	25°36.42′				

complicated. In that way, the klint forests represent some still preserved forest stands where human impact has been comparatively weak. By the Estonian Nature Information System database, 90.6% (453 ha) of the total area of klint forests has been taken under protection.

The aim of the current paper was (i) to study the soil conditions on the klint talus slopes, (ii) to describe the diversity and characteristic features of the klint forests, (iii) to analyse the mutual relationship between the soils and vegetation in these forests and, (iv) to compare Estonian forests connected with the klint with corresponding communities in a wider geographical context.

Material and methods

Field study

After a preliminary inventory of klint forest habitats, areas for vegetation and soil sampling were established, considering that (i) the size of a forest stand is at least 0.5 ha and, (ii) the stand is in natural state, i.e. has trees of all possible age classes and lacks obvious human impact. Altogether 27 sample areas were selected; all of them were located on the North Estonian (Ordovician) Klint except one, which was situated on the West Estonian (Silurian) Klint (Fig. 1). In some cases, when the forest structure on sample area was obviously different in western and eastern sides along the klint, the area was divided into two. Geographical coordinates of sample areas, represented in Fig. 1, were estimated in the centre of respective sites by means of GPS receiver.

In every sample area vegetation was analysed separately on several sample plots established (i) on the upper part of the talus slope, 4–5 m down from the outcrops lower edge or from the upper edge of terrace if the bare outcrop was lacking; (ii) on the middle part of the slope if the slope was long enough to follow the changes in forest structure, (iii) on the foot of the talus slope and,

(iv) on the talus wall if that was present. All in all, 79 sample plots with the size of about 10 × 40 m were established across the height gradient.

In every sample plot parallel to the longest sides of plot short transects of five to ten 1 × 1 m sample quadrats were laid out according to the ground vegetation heterogeneity. Distance between the quadrats along the transects was chosen randomly within the limit of 5–10 steps. On sample quadrats the projective cover of all herb and moss layer species was estimated. For multivariate analysis the average data over transects were used. If some additional species were recorded outside sample quadrats, they were introduced into species list and in data processing considered conditionally with coverage of 0.1%. Bryophytes growing on tree stems, decaying windthrown trees or rocks were registered separately and not involved to statistical analysis in the current paper.

Tree layer was characterised on the basis of their species average basal area at breast height (m^2 ha^{-1}) estimated by means of basal area gauge. Counts were carried out once or twice in the centre of transects as well as in their both ends. In five randomly chosen points, in the radius of 2 m all stems of shrub species were counted. Young trees (saplings) with a height of < 4 m and/or with a diameter of < 5 cm at breast height (1.3 m) were also interpreted as belonging to the shrub layer. For further analysis, again, the average data was used. Shrub species outside the quadrats were taken into account with a value of one.

For the morphological description of the soils, a pit was dug in the middle of 68 sample plots. Soils were classified according to the morphological characteristics and texture class of the diagnostic horizons; if necessary, the properties estimated in the laboratory were taken into account. In the laboratory, the following soil properties were estimated: (i) pH_{H2O}, (ii) pH_{KCl}, (iii) percentage of organic C content measured by oxidation of all organic matter with $K_2Cr_2O_7$ (Vorob'eva 1998); from this also the percentage of humus content was calculated, (iv) percentage of total nitrogen measured using the Kjeldahl method (van Reeuwijk 1995), (v) percentage of free carbonates by titration (ISO 10693 1994), (vi) soil specific surface area (m^2 g^{-1}) by the water steam adsorption method (Klute 1986). All analyses were performed from the fine soil fraction with a diameter less than 2 mm.

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

Data processing

At first, the principal component analysis of vegetation data was carried out and ten first principal components describing 44.7% of the total variation were used as input for cluster analysis. Then, cluster analysis was performed using the minimal incremental sum of squares algorithm (Podani 2000), employing the Euclidean distance as the measure of dissimilarity. The clusters (= community types) were established on the basis of dendrogram. Objectivity of relevés clustering was tested by classificatory discriminant analysis (StatSoft Inc. 2001).

The indicator values of the species in clusters were calculated using the Dufrêne and Legrendre (1997) method included in the program package PC-ORD, ver. 4 for Windows (McCune & Mefford 1999). The statistical significance of the obtained indicator values was evaluated with the Monte Carlo permutation test.

As the length of the gradient by species data appeared to be 4.04 SD, all 79 relevés were ordinated using a detrended correspondence analysis method (ter Braak & Šmilauer 2002) with detrending-by-segments and down-weighting of rare species. For joint ordination of 68 relevés and soil properties, detrended canonical correspondence analysis was performed (ter Braak & Šmilauer 2002). Rare species were again downweighted; soils A-horizon pH_{H2O} and humus content values which are highly correlated ($r > 0.95$) with some other soil properties were excluded from data processing.

Difference of Rendzic Leptosols properties at various heights of the talus slope was tested with ANOVA, while difference of soil properties between soils of different types was evaluated by means of discriminant analysis (StatSoft Inc. 2001).
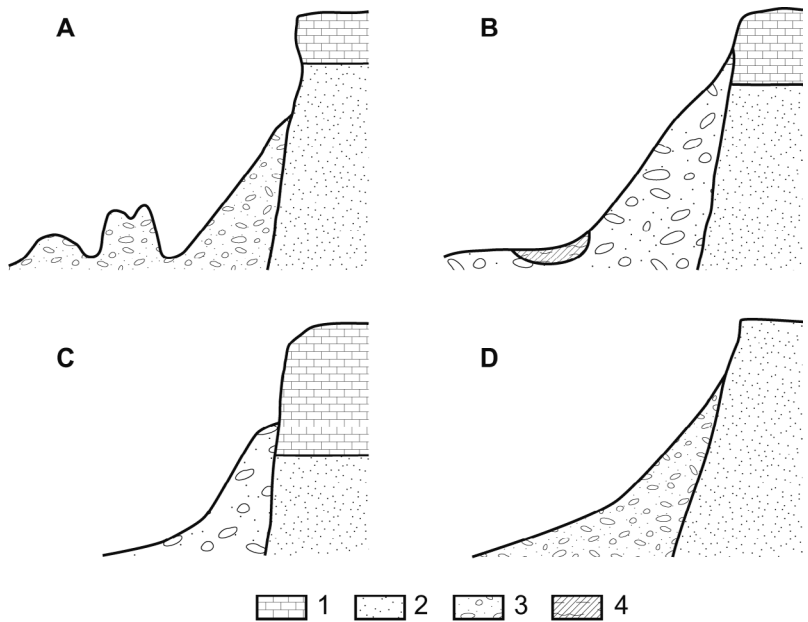
Fig. 2. Sketch of the klint profiles at (**A**) Toila, (**B**) Muuksi, (**C**) Rannamõisa and (**D**) Kunda. Notations: 1 = limestone rocks, 2 = sandstones and clastic rocks, 3 = talus slope and talus walls, 4 = Gleysols or Histosols.

Results

Water and soil conditions

The soil formation conditions differ essentially on various parts of the klint. They depend mainly on the height of the klint and on to which height (up to which strata) the escarpment is covered by talus, talus slopeness, and water conditions. Vertical extension of the talus slope is determined with the relative height of the escarpment. In places, especially in the eastern part of the klint, where its height is 50 m and more, scree will cover about 2/3 of the escarpment and has an inclination of 35°–45°. Between the klint and seashore one or two talus walls are often formed (Fig. 2A) due to the landslide on Cambrian blue clay (Miidel 1992). In the north-western part where the escarpment is lower, the scree may cover almost all of it; here the declivity is also smaller, 25°–35° (Fig. 2B). If the klint has several terraces, the talus slope occurs only along the northernmost terrace and contains eluvial deposits of the lower strata, while the southernmost terraces are overburdened.

The chemical properties of soils on talus slope and on talus walls are determined first of all by the strata represented in the escarpment profile but also by the longevity and intensity of weathering. The soils are most various in the beginning of their formation on the escarpment foot as they contain eluvial deposits from all strata. When the talus slope gradually increases, it will cover the former exposed parts of the lower strata, and in that way the younger parts of talus will get a more homogeneous content. The soil variation is less also in the case of a multiterraced klint when the northernmost terrace is built up by sandstones almost not including carbonates.

The talus walls are supplied mainly by precipitation water. On talus slopes surface water flowing down and ground water seeping out from the escarpment can be added. A very important fact is that ground water seeping on talus contains amply dissolved carbonates creating in that way favourable conditions for growth of many plant species demanding calcareous soil. Ground water seepage from the escarpment depends on the presence of water holding clay strata and the height of the slope in relation to the clay strata. If for example, ground water is running off above the talus slope upper border and the runoff is intensive enough to carry clay particles, the latter

will sediment in the upper part of the slope and cause there clay or sandy clay patches with a diameter of tens of meters. As a result, gleyic or gley soil formations can be developed in those localities (Rooma & Paal 2001).

Most common soils on talus slopes and also on talus walls are Rendzic Leptosols (Table 1). They are lacking only on sandstone screes. These soils contain numerous limestone blocks, in some places also pebbles and are very rich in carbonates. The texture of the fine soil fraction is mainly light or medium sandy loam, in some places in upper parts of the talus the texture may even be loam. The litter horizon is lacking as it disintegrates in the course of the winter. Thickness of the humus horizon is usually over 30 cm and it is laying on bedrock. On various heights on talus slope the properties of Rendzic Leptosols differ to some extent, but according to ANOVA not significantly.

On the basis of soil cover peculiarities the studied sites of the klint can be divided into six soil complexes (*sensu* Fridland 1972). The first of them is present on sites where the escarpment and talus slope are the highest (Kalvi, Purtse, Saka, Ontika, Toila). Above the talus, in addition to limestone also deeper laying strata of sandstone and interstitial clay and sandy clay strata occur in the escarpment profile (Fig. 2A). In front of the talus slope there are one or two

talus walls, in some places also dune walls. The slope is very deep and stony, it includes abundant limestone plates with a diameter of 1 m and more. In the upper part of the slope where the seeping ground water has a direct impact, the Rendzic Leptosols are interchanged with Calcaric Gleysols and Gleyic-Rendzic Leptosols. For the latter soils rather low nitrogen, carbon and carbonate content is characteristic (Table 1) as the talus surface is covered with new falls of unweathered rocks. On the lower half of the slope, plenty of ground water seeps through. There, and on talus walls pebble Rendzic Leptosols prevail; the average content of carbonates (6.4%) is here comparatively low due to the intermixing of different debris.

The second soil complex is characteristic for escarpments separated from the seashore by a coastal plain of different width (200 m to 3 km). The talus slope extends higher than the lowermost edge of the limestone strata (Fig. 2B) and the ground water does not seep on the slope (Kolga N, Muuksi, Tsitre, Valkla, Ülgase, Muraste, Suurupi). Almost all slope is covered by Rendzic Leptosol, gleyic or gley formations are lacking. Usually on the foot of the escarpment where the coastal plain begins, Eutric Gleysols or Eutric Histosols are common.

The third soil complex is the most homogeneous: only Rendzic Leptosols occur here. It can

Table 1. Average values ± SD of the uppermost horizon (A, AT) properties in different soils along the North-Estonian Klint. pH_{KCl} and pH_{H2O} = soil pH in KCl and water solution; SSA = soil specific surface area (m² g⁻¹), LOI = loss on ignition.

Property	Soil type (number (number of pits), name)						
	1 (40) Rendzic Leptosols	2 (5) Gleyic-Rendzic Leptosols	3 (8) Eutric Cambisols	6 (2) Dystric Cambisols	4 (3) Calcaric Gleysols	5 (3) Eutric Gleysols	7 (7) Eutric Histosols
	A	A	A	A	A	AT	T
pH_{H2O}	7.1 ± 0.2	7.1 ± 0.5	7.2 ± 0.6	5.1 ± 0.1	7.1 ± 0.5	7.4 ± 0.3	6.4 ± 0.2
pH_{KCl}	6.9 ± 0.2	6.7 ± 0.7	7.0 ± 0.6	4.4 ± 0.2	6.9 ± 0.4	7.2 ± 0.2	6.2 ± 0.2
N (%)	0.8 ± 0.4	0.2 ± 0.1	0.5 ± 0.2	0.3 ± 0.0	0.4 ± 0.5	0.6 ± 0.1	2.0 ± 0.2
C (%)	10.0 ± 5.5	2.7 ± 0.5	7.3 ± 5.5	3.7 ± 0.3	5.8 ± 7.7	8.1 ± 2.1	26.9 ± 3.2
C:N	12.8 ± 2.4	12.2 ± 3.9	12.8 ± 4.4	13.2 ± 0.5	13.2 ± 1.9	14.4 ± 6.3	13.4 ± 0.8
Humus (%)	17.2 ± 9.5	4.7 ± 0.9	12.7 ± 9.5	6.4 ± 0.6	9.9 ± 13.3	14.0 ± 3.7	31.5
Carbonate (%)	13.0 ± 8.5	5.4 ± 2.5	–	–	7.2 ± 1.8	–	–
SSA (m² g⁻¹)	225.1 ± 107.3	76.9 ± 32.7	158.4 ± 92.5	63.5 ± 9.4	117.0 ± 99.0	188.7 ± 50.2	–
LOI (%)	–	–	–	–	14.6	26.3 ± 6.0	65.6 ± 7.0

be found in the western part of the klint where talus slope covers the escarpment nearly up to the upper edge (Fig. 2C), ground water is not seeping on slope — it will run out on the slope foot or infiltrate deeper (Leetse, Türisalu, Laulasmaa, Rannamõisa, Jälgimäe, Nõmmeveski, Kolga W).

The fourth soil complex is presented on the West-Estonian Silurian Klint (Salevere), where the talus slope is also covered mainly by Rendzic Leptosols but the soil differs remarkably from those on the North-Estonian Ordovician Klint by the much higher average content of carbonates (up to 39.9%). This is obviously connected with the klint profile, formed in its full thickness by carbonate rocks; the upper part is made from dolomitisized limestones resistant for weathering (Raukas & Teedumäe 1997, Suuroja 2000, 2006).

When the klint has several terraces, forest vegetation grows only on the talus slope of the northernmost terrace consisting mainly of carbonate-free sandstone (Aseri, Lontova, Kunda). As the upper limestone strata are lacking, the escarpment and the talus slope are comparatively low. Usually the scree extends up to the upper border of the escarpment or is only a couple of meters lower (Fig. 2D). Soil parent material, initially poor in carbonates and nutrients, has been later enriched by seeping ground water rich in bases and nutrients and in this way particular Eutric Cambisols have been formed. The foot of the talus slope is comparatively flat and wide, here the Eutric Gleysols are common. These soils represent the fifth soil complex.

On some short sections of the sandstone escarpment where seeping ground water enriched with carbonates is lacking (Aseri), Dystric Cambisols can develop and constitute the sixth klint soil complex. pH of Dystric Cambisols is remarkably lower in comparison with other soil types (Table 1).

According to discriminant analysis, soil types differ significantly by uppermost horizon pH_{KCl} ($p < 0.001$), content of carbonates ($p < 0.001$) and specific surface area ($p = 0.039$).

Floristic content

Dominating species in the tree layer are *Ulmus glabra*, *Fraxinus excelsior*, *Tilia cordata*, *Alnus incana* and *Acer platanoides*. In some places also *Picea abies* or *Betula pendula* grow rather abundantly. On the gentle slopes at the escarpment foot on dryer habitats *Alnus incana* and on hydromorphic soils (Fig. 2B) stands of *A. glutinosa* are found. All in all, in the tree layer 17 species were found. Species number for the shrub layer was 24, including tree saplings. In the shrub layer species such as *Ribes alpinum*, *R. nigrum*, *R. rubrum*, *Corylus avellana*, *Lonicera xylosteum* and *Padus avium* prevail.

In comparison with other forest site types, the ground vegetation, especially the moss layer, on talus slopes and on their foot is remarkably species rich due to the abundance of different growth substrates (rocks, old trees, decaying wood), carbonate rich soils and good water supply (Ingerpuu *et al.* 2001). In the herb layer 123 species were recorded. The highest projective cover and frequency have *Aegopodium podagraria*, *Matteuccia struthiopteris*, *Mercurialis perennis*, *Lunaria rediviva*, *Galeobdolon luteum*, *Impatiens parviflora*, *Urtica dioica*, etc. (Appendix). In the moss layer 69 species were registered. In the forest floor *Eurynchium hians*, *E. angustirete*, *Brachythecium rutabulum*, *Rhytidiadelphus triquetrus*, *Plagiomnium cuspidatum* and *Fissidens gracifolius* have the highest cover; on the lower part of tree trunks *Anomodon longifolius*, *Pylaisia polyantha*, *Radula complanata* and *Neckera pennata* are characteristic. On limestone rocks the most frequent moss species are *Homalothecium sericeum*, *Tortula* spp. and *Encalypta* spp. These microhabitats suite well also for *Homomallium incurvatulum* and *Seligeria* spp. On limestone outcrops permanently inundated by seeping ground water *Cratoneuron filicinum* and *Palustriella commutate* are common. On sandstones, in dependence on moisture conditions, typical moss species are *Leptobryum pyriforme*, *Conocephalum conicum*, *Pohlia cruda*, *P. wahlenbergii* (Ingerpuu & Vellak 2007).

Community types

Cluster analysis resulted in 11 community types (Appendix). According to the discriminant analysis classification matrix, relevés are classified
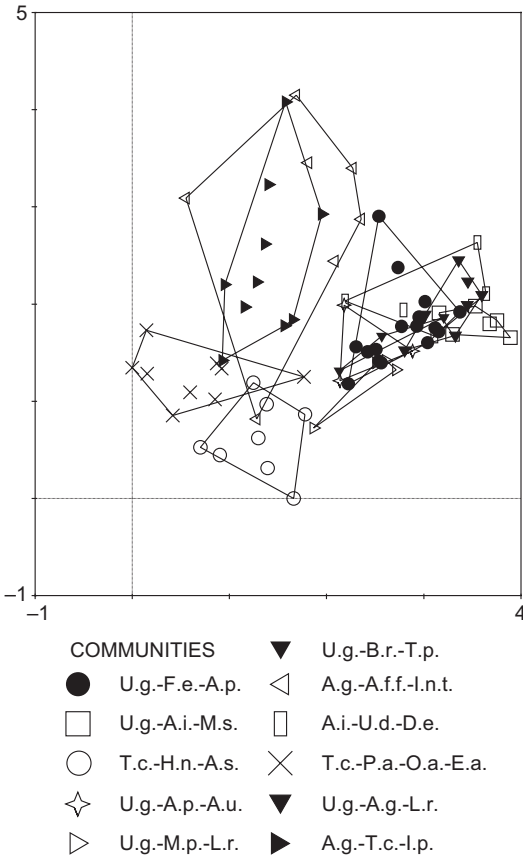
Fig. 3. Ordination of the klint forest communities by detrended correspondence analysis. Notations: U.g.-F.e.-A.p. = *Ulmus glabra–Fraxinus excelsior–Aegopodium podagraria* type, U.g.-A.i.-M.s. = *Ulmus glabra–Alnus incana–Matteuccia struthiopteris* type, T.c.-H.n.-A.s. = *Tilia cordata–Hepatica nobilis–Actea spicata* type, U.g.-A.p.-A.u. = *Ulmus glabra–Acer platanoides–Allium ursinum* type, U.g.-M.p. = *Ulmus glabra–Mercurialis perennis* type, U.g.-B.r.-T.p. = *Ulmus glabra–Brachythecium rutabulum–Thuidium philibertii* type, A.g.-A.f.f.-I.n.t. = *Alnus glutinosa–Athyrium filix-femina–Impatiens noli-tangere* type, A.i.-U.d.-D.e. = *Alnus incana–Urtica dioica–Dryopteris expansa* type, T.c.-P.a.-O.a.-E.a. = *Tilia cordata–Picea abies–Oxalis acetosella–Eurhynchium angustirete* type, U.g.-A.g.-L.r. = *Ulmus glabra–Alnus glutinosa–Lunaria rediviva* type, A.g.-T.c.-I.p. = *Alnus glutinosa–Tilia cordata–Impatiens parviflora* type.

100% correctly and the significance level for Mahalanobis distance between the community type centroids is in all cases < 0.001. For every established community type certain dominating species are characteristic as well as statistically

reliable indicator species. On that basis we can name these types as:

1. *Ulmus glabra–Fraxinus excelsior–Aegopodium podagraria* type,
2. *Ulmus glabra–Alnus incana–Matteuccia struthiopteris* type,
3. *Tilia cordata–Hepatica nobilis–Actea spicata* type,
4. *Ulmus glabra–Acer platanoides–Allium ursinum* type,
5. *Ulmus glabra–Mercurialis perennis–Lunaria rediviva* type,
6. *Ulmus glabra–Brachythecium rutabulum–Thuidium philibertii* type,
7. *Alnus glutinosa–Athyrium filix-femina–Impatiens noli-tangere* type,
8. *Alnus incana–Urtica dioica–Dryopteris expansa* type,
9. *Tilia cordata–Picea abies–Oxalis acetosella–Eurhynchium angustirete* type,
10. *Ulmus glabra–Alnus glutinosa–Lunaria rediviva* type,
11. *Alnus glutinosa–Tilia cordata–Impatiens parviflora* type.

The 1st type embraces the largest number of communities and is present from Salevere and Leetse in western Estonia to Meriküla in northeastern Estonia. Rather frequent and comparatively widely distributed are also communities of the 3rd, 7th, 9th, 10th and 11th types. At the same time, communities of *Ulmus glabra–Acer platanoides–Allium ursinum* (4th type) were recorded mainly on western part of the Viimsi peninsula and in Kalvi. Sites with very scarce herb layer, i.e. *Ulmus glabra–Brachythecium rutabulum–Thuidium philibertii* (6th type) are first of all in Saka.

A larger interior variability is characteristic for communities of 3rd, 7th, 9th and 11th types being at the same time rather well separated in character space from communities of other types (Fig. 3). Communities of the 2nd and 5th types also do not have on the ordination plot remarkable overlapping with neighbouring communities, while communities of the remaining types seem to be syntaxonomically more continuous.

According to the frequency of soils, most communities grow on Rendzic Leptosols. Only

Ulmus glabra–Acer platanoides–Allium ursinum communities are bound to Eutric Cambisols. For *Alnus incana–Urtica dioica–Dryopteris expansa* communities Eutric Gleysols, and for *Alnus glutinosa–Athyrium filix-femina–Impatiens noli-tangere* communities Eutric Histosols are characteristic.

In several places the structure and, thus, the type of the communities changes with talus slope height. The *Tilia cordata–Hepatica nobilis–Actea spicata* type is usually found on upper parts of scree, while the *Ulmus glabra–Alnus incana–Matteuccia struthiopteris* type is characteristic for lower parts of the talus slope. Communities of *Alnus glutinosa–Athyrium filix-femina–Impatiens noli-tangere* are without exception confined to the foot of scree or to the adjacent coastal plain. The communities of *Alnus glutinosa–Tilia cordata–Impatiens parviflora* have usually a similar location. The communities of other types are to be found on various heights on the talus slope. In many sites (Leetse, Rannamõisa, Viimsi E, Ülgase, Kolga W, Nõmmeveski E, Muuksi, Kunda E, Saka) upper and lower parts of the talus slope are covered with the same community.

On talus walls grow mostly *Ulmus glabra–Fraxinus excelsior–Aegopodium podagraria* or *Ulmus glabra–Alnus incana–Matteuccia struthiopteris* communities, but also *Ulmus glabra–Acer platanoides–Allium ursinum* and *Ulmus glabra–Brachythecium rutabulum–Thuidium philibertii* communities occur (in Kalvi and Saka, respectively).

The most species-rich are the communities of *Alnus glutinosa–Athyrium filix-femina–Impatiens noli-tangere* and *Ulmus glabra–Fraxinus excelsior–Aegopodium podagraria* type, while the *Ulmus glabra–Acer platanoides–Allium ursinum* communities have notably less species than communities of other types (Appendix). The scarcity of species in latter communities results from the high fertility and good vegetative regeneration of *Allium ursinum*, preventing the growth of other species (Diekmann, 1994). Also in communities where *Matteuccia struthiopteris* (2nd type) or *Mercurialis perennis* (5th type) in field layer have a dominating position the total species number is lower than 50. The mean number of species per community is very low (14), especially in *Allium ursinum* rich communities and in communities where *Impatiens parviflora* has high cover. As expected, for communities with one prominently dominating species (*Matteuccia struthiopteris*, *Allium ursinum*, *Lunaria rediviva* or *Impatiens parviflora*) in field layer the lowest values (0.644–0.658; Appendix) of evenness coefficients are characteristic. The highest evenness (0.931), i.e. the most equal species abundance (Pielou 1977) have communities of *Alnus incana–Urtica dioica–Dryopteris expansa* type.

According to the detrended canonical correspondence analysis the two first ordination axes have eigenvalue 0.350 and 0.156, respectively, and characterize 57.1% of the species–environment (soil properties) relationship; the next ordination axes do not improve this result. The soil properties most affecting the vegetation variation, are the specific surface area and strongly correlated ($r > 0.91$, $p < 0.001$) with that, the nitrogen and carbon content (Fig. 4). Interset correlation of soil specific surface area with the first ordination axis is –0.626 and the significance of the first axis according to the Monte Carlo permutation test 0.002. Relevés variation in direction of the second ordination axis is connected mainly with the ratio of carbon and nitrogen content in soils, with their carbon content and with soils pH_{KCl} (Table 2).

Discussion

Due to the diversity of soil and moisture conditions and availability of microhabitats of various quality, the ground vegetation of klint forests, especially the moss layer, is remarkably species rich. Though the total cover of bryophytes is considerably lower than the total cover of herb species, the average ratio of the moss layer species number to the number of vascular species is approximately 1.0 in the scale of communities as well as in the scale of sample quadrats. In other forests of eutrophic boreo-nemoral type group (Paal 1997) this ratio is about 0.7 (Ingerpuu *et al*. 2001). The ratio is also considerably below 1.0 in forests of other types, the only exception being the bog forests which are very poor in vascular species. The peculiarity of klint forests is
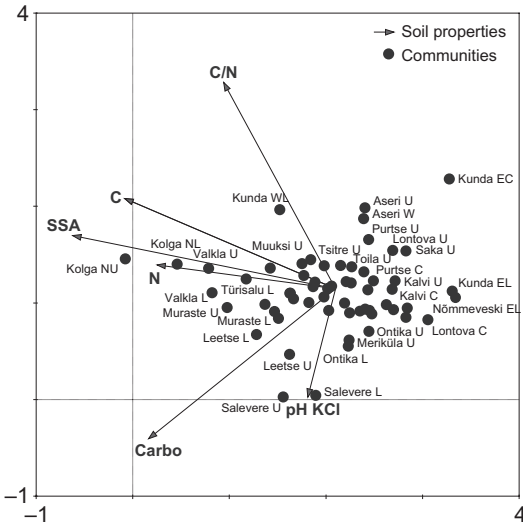
Fig. 4. Detrended canonical correspondence analysis biplot of klint forest communities and their uppermost soil horizon (A, AT) properties. Notations as in Table 1.

their surplus of rock substrates enabling numerous species adapted to that kind of microhabitats to grow here (Sjögren 1964). Among bryophytes these species constitute almost 25%. 14% of klint forest bryophytes belong to the Estonian red list species (Ingerpuu *et al.* 2001), proving the uniqueness of these communities.

From byophytes the most remarkable species is *Fissidens gracifolius*, recorded altogether in 16 sample areas out of 27. It grows in humid shaded places on limestone pieces and plates laying on soil surface. Earlier this species was registered in Estonia only in three localities (Paal *et al.* 2001). Among herb layer species the most characteristic is *Lunaria rediviva*; in other

nemoral forests this species is due to the human impact nowadays very rare (Laasimer 1975).

The diversity of forest communities connected with the North-Estonian Klint appears to be much higher than earlier authors have asserted. According to Lippmaa (1933) and Kalda (1995), the tree layer of these forests is represented only by the *Ulmus–Acer–Tilia* society, though they both mention also the occurrence of *Alnus incana* stands. Kalda (1958) distinguished *Aegopodium podagraria* society and *Mercurialis perennis* society in the herb layer of these forests. On the vegetation map of Lahemaa National Park, forests related with klint are represented only with two units identified by ground vegetation: *Mercurialis perennis–Aegopodium podagraria* type and *Galeobdolon luteum–Asperula odorata* type (Kalda 1988). Here the scarcity of types follows obviously from the restricted area of klint forests whereas on the territory of that national park they occur only in Tsitre, Muuksi and Kolga.

In our former study, based on more restricted data we classified the klint forests into six community types: (i) *Ulmus glabra–Fraxinus excelsior–Aegopodium podagraria–Eurynchium hians* type, (ii) *Alnus incana–Mercurialis perennis* type, (iii) *Ulmus glabra–Lunaria rediviva–Brachythecium rutabulum* type, (iv) *Ulmus glabra–Alnus incana–Matteuccia struthiopteris* type, (v) *Tilia cordata–Impatiens parviflora* type and, (vi) *Tilia cordata–Picea abies–Oxalis acetosella–Eurynchium angustirete* type (Paal *et al.* 2001). The 1st, 4th and 6th types correspond well to the types repeatedly estimated in the current study, while the 2nd, 3rd and 5th community types have very similar herb and moss layers with *Ulmus glabra–Mercurialis perennis*, *Ulmus glabra–Alnus glutinosa–Lunaria rediviva*, and *Alnus glutinosa–Tilia cordata–Impatiens parviflora* types, respectively, established in the current study; only some changes or additions in the tree layer dominant species have occurred.

Ground vegetation of *Ulmus glabra–Acer platanoides–Allium ursinum* communities is very similar to that of communities growing on levees of Estonian floodplains on Eutric Gleysols or Gleyic Fluvisols but there, instead of *Ulmus glabra* and *Acer platanoides*, usually *Ulmus laevis* is prevailing in the tree layer. On flood-

Table 2. Eigenvalue of three first ordination axes and interset correlation of soil properties with them according to the detrended canonical correspondence analysis. Notations as in Table 1.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.360	0.156	0.097
pH_{KCl}	−0.054	−0.407	−0.361
N (%)	−0.429	0.078	0.043
C (%)	−0.505	0.244	−0.053
SSA	−0.626	0.132	−0.103
Carbonate (%)	−0.445	−0.432	−0.315
C:N	−0.260	0.482	−0.430

plain terraces, on temporarily overmoistened or even flooded Dystri-Gleyic Arenosols quite convergent communities with *Ulmus glabra–Mercurialis perennis* type can also be found, but there *Tilia cordata* dominates in tree layer (Paal *et al*. 2007, 2008).

In the distribution of different communities we can follow certain regularity. Communities with very dense growth of *Matteuccia struthiopteris* occur east from Kunda (Fig. 1), where talus slopes are covered with limestone blocks and debries. Westward only single synusia of this fern can be found. In a similar way *Lunaria rediviva* has also an eastern distribution and does not occur further to the west from Ülgase. Lack of that species westwards from Tallinn was pointed out already by Lippmaa (1935). *Mercurialis perennis* dominated communities are not present in the easternmost parts of the klint, in Toila and Meriküla. From Aseri eastwards also communities of *Tilia cordata–Picea abies–Oxalis acetosella–Eurynchium angustirete* type are rare.

In addition to old and big stems of *Ulmus glabra* (maximal diameter at breast height in Saka 69 cm), *Tilia cordata* (89 cm in Leetse) and *Alnus glutinosa* (62 cm in Valkla), in some stands *Alnus incana* (in Kunda E 42 cm, in Kunda W and Aseri 40 cm) have remarkable diameters. Talus slopes of the klint and floodplain levees are the only habitats in Estonia where *A. incana* can have a primary dominating position in the tree layer (Lippmaa 1935, Paal *et al*. 2007). Therefore, the respective stands together with old-growth *Ulmus glabra* and *Tilia cordata* communities have a very high value from the biodiversity point of view.

Eutrophic *Ulmus glabra–Fraxinus excelsior* forests analogous to the Estonian *Ulmus glabra* rich stands on the talus slopes can be found in different parts of the boreo-nemoral and nemoral zones in southern Scandinavia (Sjögren 1961, 1964, Diekmann 1994, 1999, Dierβen 1996). There these forests grow both on level ground and on slopes of varying aspect and steepness but are mostly bound to the areas with calcareous bedrock and/or rich glacial deposits. The soils are usually loamy or clayey and very nutrient-rich (Klötzli 1975a). Within the nemoral zone in Skåne, southern Sweden, they are characterized *inter alia* by *Lunaria rediviva* (Diekmann 1994,

1999). Diekmann (1994) divided *Ulmus glabra–Fraxinus excelsior* type into *Allium ursinum* subtype and *Gagea lutea* subtype. The former subtype corresponds rather well to the Estonian *Ulmus glabra–Acer platanoides–Allium ursinum* communities and at least partly to the *Ulmus glabra–Mercurialis perennis* communites as in *Allium ursinum* subtype *Mercurialis perennis* is often a codominant species. Single similar stands, named by Kielland-Lund (1981) as *Ulmo–Tilietum* communities with *Allium*, are also located in warm mountainous places on calcareous bedrock in south-eastern Norway.

In central Europe analogous communities are represented by *Fraxino–Aceretum* association having several subassociations (Ellenberg 1996). Two of these are differentiated by *Lunaria rediviva*, and *Allium ursinum* together with *Ranunculus lanuginosus*. Earlier by Oberdorfer (1957) the communities with characteristic *Lunaria rediviva* have been treated among calcareous ravine forests as *Ulmeto–Aceretum lunarietosum* Kuhn 37 = *Phyllitio–Aceretum* Moor 52. In scope of that association Ellenberg (1996) established also a subassociation bound to coarse shingle without having any differential species (bryophytes were ignored). Due to the lack of field layer those communities are similar with communities of *Ulmus glabra–Brachythecium rutabulum–Thuidium philibertii* type even though dominant species in the tree layer are not the same.

The klint forests dominated by *Tilia cordata* have a great affinity with South Scandinavian mesotrophic *Quercus robur–Tilia cordata* stands on steep, boulder-rich slopes and screes though the bottom layer of these communities varies considerably (Diekmann 1994). Respective habitats have a fairly good supply of base rich material and nutrients (Klötzli 1975a). Dierβen (1996) also stresses that the lime dominated stands of *Ulmo glabrae–Tilietum cordatae* association are related to warm slopes of southern or south-western exposition. In many places, ground water comes to the surface, creating more or less stable moisture conditions, causing a permanent transport and enrichment of minerals and nutrients, and preventing the leaching of the soil (Sjörs 1967). Rühl (1960) and Mayer (1984) pointed out similarity of the Estonian

Tilio cordatae–Ulmetum glabrae type communities with the central European *Acero–Tilietum* association. According to Ellenberg (1996), the lime-rich mixed forests are growing there on stony but dry slopes.

A certain similarity can be observed between the Estonian communities of *Alnus incana–Urtica dioica–Dryopteris expansa*, *Ulmus glabra–Alnus incana–Matteuccia struthiopteris*, *Alnus glutinosa–Athyrium filix-femina–Impatiens noli-tangere* and *Alnus glutinosa–Tilia cordata–Impatiens parviflora* on talus slopes with vicariant fern rich alder–ash forests in the boreonemoral zone of Fennoscandia and Russia, confined to gently or moderately sloping ground at the foot of slopes and along brooks or small rivers (Runemark 1950, Tapio 1953, Diekmann 1994, Fremstad 1997, Fedorchuk *et al.* 2005). The term 'alder–ash forests' will also be used for *Alnus glutinosa* and *A. incana* forests without *Fraxinus* (Diekmann 1994). When in Scandinavian alder–ash forests *Tilia cordata* is completely absent (Diekmann 1994), then in Estonia, at least in *Alnus glutinosa–Tilia cordata–Impatiens parviflora* communites, it has a dominant position. Respective forests in Sweden have been also treated as *Alno–Ulmetum* (Klötzli 1975a, 1975b), in Norway as *Alno incanae–Prunetum padi* (Kielland-Lund 1981, 1994, Diekmann 1994), hillside *Alnus incana* forests (Fremstad & Øvstedal 1978) or *Alno incanae–Fraxinetum* (Dierβen 1996), and they occur from eastern to western Norway and north to Finnmark (Kielland-Lund 1994, Fremstad 1997). In southern Scandinavia *Alnus glutinosa* is dominating in alder–ash stands, but northwards from 'limes norrlandicus' this species as well as *Fraxinus excelsior* are replaced by *A. incana* (Dierβen 1996, Diekmann 1999). In central Europe, *Alno–Fraxinetum* forests are growing mainly in mountains along the brooks and rivers but they may also occur outside river valleys (Ellenberg 1996).

Acknowledgement

References

Aaloe, A. & Miidel, A. 1967: *Eesti pangad ja joad*. — Eesti Raamat, Tallinn.

Diekmann, M. 1994: Deciduous forest vegetation in Boreonemoral Scandinavia. — *Acta Phytogeogr. Suec.* 80: 1–112.

Diekmann, M. 1999: Southern deciduous forests. — *Acta Phytogeogr. Suec.* 84: 33–53.

Dierβen, K. 1996: *Vegetation Nordeuropas*. — Verlag Eugen Ulmer, Stuttgart.

Dufrêne, M. & Legrendre, P. 1997: Species assemblages and indicator species: the need for a flexible asymmetrical approach. — *Ecol. Monogr.* 67: 345–366.

EC 1992: Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. — *Official Journal of European Community* L206: 7–50.

Ellenberg, H. 1996: *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*. — Verlag Eugen Ulmer, Stuttgart.

Fedorchuk, V. N., Neshatayev, V. Yu. & Kuznetsova, M. L. 2005: *Forest ecosystems of the north-western regions of Russia: typology, dynamics, forest management features*. — Sankt-Peterburgskij nauchno-issledovatel'skij institut lesnogo hozyajstva, Sankt-Peterburg. [In Russian with English summary].

Fremstad, E. 1997: Vegetasjontyper i Norge. — *NINA Temahefte* 12: 1–279.

Fremstad, E. & Øvstedal, D. O. 1978: The phytosociology and ecology of grey alder (*Alnus incana*) forests in central Troms, North Norway. — *Astarte* 11: 93–112.

Fridland, V. M. [Фридланд, В. М.] 1972: [*Stucture of soil cover*]. — Mysl', Moskva. [In Russian].

Gruner, L. 1864: Versuch einer Flora Allentackens und des im Süden angrenzenden Theiles von Nord-Livland. — *Archiv für die Naturkunde Liv-, Ehst- und Kurlands*, Bd. 6, Ser. 2: 373–532.

Hinneri, S. 1972: An ecological monograph on eutrophic deciduous woods in the SW archipelago of Finland. — *Ann. Univ. Turkuensis* A II 50: 1–131.

Ingerpuu, N., Vellak, K., Liira, J. & Pärtel, M. 2001: Relationships between species richness in deciduous forests at the north Estonian limestone escarpment. — *J. Veg. Sci.* 14: 773–780.

Ingerpuu, N. & Vellak, K. (eds.) 1998: *Eesti sammalde määraja*. — EPMÜ ZBI & Eesti Loodusfoto, Tartu.

Ingerpuu, N. & Vellak, K. 2007: Klint sammalde elupaigana. — In: Puura, I., Pihu, S. & Amon, L. (eds.), *XXX Eesti loodusuurijate päev. Klindialade loodus*: 64–74. Eesti Looduseuurijate Selts, Tartu.

ISO 10693 1994: *Soil quality — Determination of carbonate content — Volumetric method*. — International Organization for Standardization, Geneva, Switzerland.

Jalas, J. 1957: Die geobotanische Nordostgrenze der sog.

Eichenzone Südwestfinnlands. — *Ann. Bot. Soc. Vanamo* 29: 1–32.

Kalda, A. 1958: Laialehiste lehtmetsade kaasaegne levik Eesti NSV-s. — *TRÜ Toimetised* 64. *Botaanika-alased tööd* 1: 102–114.

Kalda, A. 1960: Eesti NSV laialehiste metsade taimkate. — *TRÜ Toimetised* 93. *Botaanika-alased tööd* 4: 123–155.

Kalda, A. 1962: Laialehised metsad Eestis. — In: Rebane, H. (ed.), *Salumetsade majandamise küsimusi*: 129–137. ENSV TA ZBI, Tartu.

Kalda, A. 1988: Lahemaa Rahvuspargi taimkate ja selle geobotaaniline liigestus. — In: Etverk, I. (ed.), *Lahemaa uurimused*, vol 3: 68–87. Valgus, Tallinn.

Kalda, A. 1995: Broadleaved deciduous forests of Estonia. — *Scripta Botanica* (Tartu University) 9: 89–95.

Kalela, A. 1954: Waldvegetationszonen Finnlands und ihre klimatischen Paralleltypen. — *Arch. Soc. Vanamo* 16 (Suppl.): 65–83.

Kielland-Lund, J. 1981: Die Waldgesellschaften SO-Norwegens. — *Phytocoenologia* 9: 53–250.

Kielland-Lund, J. 1994: Syntaxonomy of Norwegian forest vegetation. — *Phytocoenologia* 24: 299–310.

Klute, A. (ed.) 1986: *Methods of soil analysis. Part 1. Physical and mineralogical methods*. — Soil Science Society of America & American Society of Agronomy, Madison, Wisconsin, USA.

Klötzli, F. 1975a: Edellaubwälder im Bereich der südlichen Nadelwälder Schwedens. — *Ber. Geobot. Inst. ETH Stiftung Rübel* 43: 23–53

Klötzli, F. 1975b: Zum Standort von Edellaubwäldern im Bereich des südlichen borealen Nadelwaldes. — *Mitteilungen der Eidgenössischen Anstalt für das forstliche Versuchswesen* 51: 49–64.

Laasimer, L. 1962: Salumetsatüüpidest. — In: Rebane, H. (ed.), *Salumetsade majandamise küsimusi*: 116–135. ENSV TA ZBI, Tartu.

Laasimer, L. 1965: *Eesti NSV taimkate*. — Valgus, Tallinn.

Laasimer, L. 1975: Haruldaste taimekoosluste olukord ja kaitse probleemid Eestis. — In: Renno, O. (ed.), *Eesti loodusharulduste kaitseks*: 20–35. Valgus, Tallinn.

Leht, M. (ed.) 2007: *Eesti taimede määraja*. — EMÜ & Eesti Loodusfoto, Tartu.

Lippmaa, T. 1933: Taimeühingute uurimise metoodika ja Eesti taimeühingute klassifikatsiooni põhijooni. — *Acta Instituti et Horti Botanici Universitatis Tartuensis (Dorpatensis)* 3: 1–169.

Lippmaa, T. 1935: Eesti geobotaanika põhijooni. — *Acta Instituti et Horti Botanici Universitatis Tartuensis* 4: 3–151.

Lõhmus, E. 2004: *Eesti metsakasvukohatüübid*. — Eesti Loodusfoto, Tartu.

Masing, V. 1966: Metsatüpoloogia probleeme. — In: Trass, H. (ed.), *Loodusuurijate Seltsi Aastaraamat* 59: 150–169. Valgus, Tallinn.

Mayer, H. 1984: *Wälder Europas*. — Gustav Fischer Verlag, Stuttgart.

McCune, B. & Mefford, M. J. 1999: *PC-ORD. Multivariate analysis of ecological data*, ver. 4. — MjM Software Design, Gleneden Beach, Oregon, USA.

Miidel, A. 1992: Balti klindi päritolu. — *Eesti Loodus* 2: 77–81.

Miidel, A. 1997: Escarpments and waterfalls. — In: Raukas, A. & Teedumäe, A. (eds.), *Geology and mineral resources of Estonia*: 391–395. Estonian Academy Publishers, Tallinn.

Oberdorfer, E. 1957: *Süddeutsche Pflanzengesellschaften*. — Pflanzensoziologie, Bd 10. VEB Gustav Fischer Verlag, Jena.

Paal, J. 1997: *Eesti taimkatte kasvukohatüüpide klassifikatsioon*. — Keskkonnaministeerium & ÜRO Keskkonnaprogramm, Tallinn.

Paal, J. 1998: Rare and threatened plant communities of Estonia. — *Biodiversity and Conservation* 41: 11–37.

Paal, J. 2007: *Loodusdirektiivi elupaigatüüpide käsiraamat*. — Auratrükk, Tallinn.

Paal, J., Prieditis, N., Rannik, R. & Jeletsky, J. 2008: Classification structure of floodplain forests in Estonia: a comparison of two classification approaches. — *Annales Botanici Fennici* 45: 255–268.

Paal, J., Rannik, R., Jeletsky, E.-M. & Prieditis, N. 2007: Floodplain forests in Estonia: Typological diversity and growth conditions. — *Folia Geobotanica* 42: 383–400.

Paal, J., Vellak, K. & Ingerpuu, N. 2001: The species composition of Estonian klint forests, their classification and their correlation with the main soil parameters. — *Forestry Studies* 35: 104–132. [In Estonian with English summary].

Pielou, E. C. 1977: *Mathematical ecology*. — John Wiley & Sons, New York.

Podani, J. 2000: *Introduction to the exploration of multivariate biological data*. — Backhuys Publishers, Leiden.

Raukas, A. 1996: Location, topography and geological structure. — In: Raukas, A. (ed.), *Estonian environment: past, present and future*: 7–14. Ministry of the Environment of Estonia & Environment Information Centre, Tallinn.

Raukas, A. & Teedumäe, A. (eds.) 1997: *Geology and mineral resources of Estonia*. — Estonian Academy Publishers, Tallinn.

Rooma, I. & Paal, J. 2001: Soils of Estonian klint forests. — In: Möls, T., Kalda, A., Kongo, L. & Reintam, L. (eds.), *Year-book of the Estonian Naturalists' Society*, vol. 80: 178–209. Estonian Academy Publishers, Tallinn. [In Estonian with English summary].

Runemark, H. 1950: Forests with a field layer dominated by high-grown ferns. — *Botaniska Notiser* 1950 2: 230–233.

Russow, E. 1864: Flora der Umgebung Revals. — *Archiv für die Naturkunde Liv-, Ehst- und Kurlands*, Bd. 6, Ser. 2: 1–120.

Russow, E. 1889: Ueber die Boden- und Vegetationsverhältnisse zweier Ortschaften an der Nordküste Estlands. — *Sitzungsberichte der Naturforscher-Gesellschaft* 8: 93–142.

Rühl, A. 1960: Über die Waldgesellschaften Estlands. — *Annales Societatis Litterarum Estonicae in Svecia* 3: 44–55.

Schmidt, F. 1859: Flora des silurischen Bodens von Ehstland, Nord-Livland und Oesel. — *Archiv für die Naturkunde Liv-, Ehst- und Kurlands*, Bd. 1, Ser. 2: 149–260.

Sjögren, E. 1961: Epiphytische Moosvegetation in Laubwäl-

dern der Insel Öland (Schweden). — *Acta Phytogeographica Suecica* 44: 1–149.

Sjögren, E. 1961: Epiphytische und Epigäische Moosvegetation in Laubwäldern der Insel Öland (Schweden). — *Acta Phytogeographica Suecica* 48: 1–184.

Sjörs, H. 1967: *Nordisk växtgeografi*. — Svenska Bokförlaget Bonniers, Stockholm.

StatSoft Inc. 2001: *STATISTICA (data analysis software system)*, ver. 6. — www.statsoft .com.

Suuroja, K. 2000: Balti klint. — *Loodus* 1: 44–51.

Suuroja, K. 2006: Baltic Klint in North Estonia as a symbol of Estonian nature. — Ministry of Environment, Tallinn.

Tammekann, A. 1940: The Baltic glint. — *Acta ad Res Naturae Estonicae Perscrutandas*, Ser. 1(11): 1–104.

Tapio, S. 1953: Tutkimuksia lehtokasvillisuudesta ja lehtokasvien ekologisesta ryhmittymisestä Pirkkalan lehtokeskuksen keskiosassa. — *Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo* 25: 1–57.

ter Braak, C. J. F. & Šmilauer, P. 2002: *CANOCO reference manual and CanoDraw for Windows user's guide*. — Biometris, Wageningen & České Budějovice.

van Reeuwijk, L. P. (ed.) 1995: *Procedures for soil analysis*. — ISRIC, Wagening.

Vorob'eva, L. A. [Воробьева, Л. А.] 1998: [*Chemical analysis of soils*]. — Izdatel'stvo Moskovskogo Universiteta, Moskva. [In Russian].

WRB 2006: World reference base of soil resources. — *World Soil Resources Reports* 103: 1–128.

Appendix. Centroids of the Estonian klint forests community types. The names of tree-layer species are capitalized, for shrub-layer species and saplings only the genus name is capitalized. Only species with mean abundance value (basal area for trees, number of stems for saplings and shrubs, coverage percentage for herb and moss layer species) > 0.5% in at least one type are presented. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Variable, species	Community type										
	1	2	3	4	5	6	7	8	9	10	11
Number of communities	17	6	8	3	4	3	7	5	9	7	10
Evenness coefficient	0.693	0.644	0.755	0.647	0.759	0.719	0.692	0.931	0.703	0.654	0.658
Total number of species	97	49	85	21	45	50	108	58	84	58	55
Mean number of species per community	25	22	27	11	22	29	29	22	32	23	14
Number of tree layer species	13	7	10	5	8	7	11	8	12	5	8
Number of shrub layer species (saplings excluded)	8	4	8	2	5	4	8	5	9	5	5
Total cover of herb layer	65	67	26	45	42	27	63	62	22	64	54
Number of herb layer species	43	6	44	7	22	16	55	27	33	25	21
Total cover of moss layer	22	28	10	3	23	43	22	9	51	18	10
Number of moss layer species	33	22	23	7	10	23	34	18	30	23	21
Indicator species											
Aegopodium podagraria	36.8***	11.6	1.7	3.4	2.3	0.0	3.9	8.6	1.3	9.7	1.8
Matteuccia struthiopteris	7.1	55.6***	0.0	0.0	0.0	6.4	0.3	1.3	0.6	8.3	0.3
TILIA CORDATA	1.3	0.0	9.4*	0.0	3.5	0.0	0.0	0.0	5.3	2.0	5.2
LONICERA xylosteum	0.6	1.0	3.1*	0.0	1.0	2.5	0.1	0.1	2.1	1.2	0.5
Actea spicata	0.6	0.0	1.4*	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.2
Campanula trachelium	0.0	0.0	0.6*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Convallaria majalis	0.0	0.0	2.0**	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Hepatica nobilis	0.7	0.0	3.4**	0.0	0.4	0.0	0.0	0.0	0.9	0.0	0.0
Lathyrus vernus	0.2	0.0	2.3**	0.0	0.7	0.0	0.0	0.0	0.8	0.0	0.2
Polygonatum multiflorum	0.1	0.0	0.6**	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Allium ursinum	2.2	3.3	0.0	29.0**	0.0	0.0	0.0	0.0	0.0	1.0	2.0
Mercurialis perennis	10.0	4.3	1.9	10.3	26.0**	6.5	4.0	3.6	3.9	3.2	0.0
Anomodon longifolius	1.0	0.0	3.4	2.1	6.0*	0.7	0.0	0.0	0.3	1.3	0.6
ULMUS GLABRA	6.1	8.0	3.2	6.7	8.9	12.8*	0.0	1.1	1.2	5.8	1.6
Brachythecium rutabulum	2.4	3.8	0.4	0.3	6.3	22.6**	3.1	2.1	3.3	9.3	2.4
Thuidium philibertii	0.0	0.0	0.0	0.0	0.1	7.7**	0.0	0.0	0.0	0.0	0.0
ALNUS GLUTINOSA	2.4	0.0	0.1	2.7	0.6	0.0	18.0**	0.0	0.9	4.1	7.3
Athyrium filix-femina	0.0	0.0	0.0	0.0	0.0	0.0	12.9*	0.0	0.2	0.0	0.3

Appendix. Continued.

Variable, species	Community type										
	1	2	3	4	5	6	7	8	9	10	11
Crepis paludosa	0.1	0.0	0.0	0.0	0.0	0.0	3.6**	0.0	0.0	0.0	0.0
Geum rivale	0.3	0.0	0.0	0.0	0.0	0.0	3.4*	0.0	0.0	0.0	0.0
Impatiens noli-tangere	0.1	0.3	0.0	0.0	0.0	0.3	13.9*	0.1	0.0	0.3	5.1
Brachythecium rivulare	0.4	0.0	0.0	0.0	0.0	0.7	4.7*	1.4	0.0	0.3	0.1
Plagiomnium elatum	0.6	0.0	0.0	0.0	0.0	0.0	4.6*	0.3	0.0	0.1	0.0
ALNUS INCANA	2.8	6.2	0.0	0.0	1.6	2.5	0.4	17.2***	0.4	3.0	0.8
Chrysosplenium alternifolium	0.0	0.1	0.0	0.0	0.0	0.0	0.4	3.0*	0.0	0.8	0.0
Dryopteris expansa	0.1	1.8	0.0	0.0	0.0	0.0	0.2	7.4*	0.2	1.1	0.0
Urtica dioica	2.0	5.8	0.0	0.0	0.1	7.7	1.0	21.4**	0.0	3.3	0.0
PICEA ABIES	0.0	0.0	0.6	0.0	0.4	0.0	2.5	0.0	4.6**	0.0	0.0
RIBES alpinum	1.9	0.3	5.2	0.0	3.0	0.5	1.2	1.5	7.2*	0.5	1.0
TILIA cordata	0.0	0.0	1.6	0.0	0.3	0.0	0.0	0.0	2.4*	0.4	0.8
Gymnocarpium dryopteris	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1*	0.0	0.0
Eurhynchium angustirete	0.0	0.2	0.0	0.0	0.1	5.1	0.0	0.0	21.1***	0.1	0.0
Hylocomium splendens	0.0	0.0	0.1	0.0	0.0	0.0	1.1	0.0	6.3*	0.0	0.5
Rhythidiadelphus triquetrus	0.1	0.0	0.9	0.0	0.0	0.0	0.5	0.0	15.0***	0.0	0.8
Lunaria rediviva	3.5	4.3	0.0	0.0	8.4	0.0	0.0	0.0	0.0	44.7***	0.1
Impatiens parviflora	0.8	0.0	0.7	1.7	0.0	0.0	1.0	0.0	0.0	0.0	35.3***
Other species											
ACER PLATANOIDES	2.0	0.6	3.5	6.3	1.0	0.8	0.5	0.5	1.7	1.9	3.6
BETULA PENDULA	0.3	0.0	0.0	0.0	0.0	0.2	2.1	0.3	1.9	0.0	0.0
FRAXINUS EXCELSIOR	5.1	0.4	4.9	2.8	2.9	1.2	0.9	1.0	1.5	2.0	3.8
PADUS AVIUM	0.5	1.1	0.6	0.8	1.0	1.0	0.0	0.3	0.5	0.4	0.0
PINUS SYLVESTRIS	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.9	0.0	0.0
POPULUS TREMULA	0.1	0.2	0.2	0.0	0.0	0.0	0.5	1.1	0.3	0.0	0.0
SORBUS AUCUPARIA	0.6	1.3	0.2	0.0	0.3	0.5	0.6	1.9	0.6	0.0	0.1
ACER platanoides	1.1	0.1	3.6	1.4	1.6	2.7	0.2	0.1	1.3	0.4	2.8
ALNUS glutinosa	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0
ALNUS incana	1.2	2.5	0.4	0.0	1.4	2.0	0.3	1.3	0.4	0.2	0.7
CORYLUS avellana	2.1	1.4	2.9	0.0	2.4	0.4	1.0	0.5	4.2	0.4	0.3
FRAXINUS excelsior	0.9	0.2	3.4	2.3	0.3	0.2	0.9	0.7	0.7	0.3	2.7
PADUS avium	0.8	1.4	0.6	1.7	0.0	0.7	1.6	1.2	0.2	0.2	1.3
POPULUS tremula	0.1	0.2	0.2	0.0	0.0	0.0	0.3	0.4	0.6	0.0	0.0
RIBES nigrum	0.2	4.1	0.0	1.5	5.0	2.7	2.6	2.0	0.2	1.0	0.0
RIBES rubrum	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.6	0.0	0.1
ROSA spp.	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SORBUS aucuparia	0.4	0.6	0.3	0.3	0.5	0.7	0.5	1.2	0.1	0.2	0.1
ULMUS glabra	0.4	0.9	2.0	1.7	0.1	2.2	0.0	0.0	0.5	1.0	0.2
Anemone nemorosa	0.3	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Angelica sylvestris	0.0	0.0	0.4	0.0	0.0	0.1	0.1	2.1	0.0	0.3	0.0
Calamagrostis arundinacea	0.1	0.0	1.3	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0
Caltha palustris	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0
Campanula latifolia	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
Cardamine impatiens	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0
Carex acuta	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0
Carex cespitosa	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0
Chelidonium majus	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8
Cirsium oleraceum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.3	0.0
Dryopteris filix-mas	0.2	0.0	0.5	0.0	1.7	2.2	0.0	0.0	0.5	0.0	0.6
Empetrum nigrum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0
Equisetum pratense	0.2	0.0	0.0	0.0	0.0	0.0	1.0	0.4	0.0	0.0	0.1
Eupatorium cannabinum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.2	0.0	0.0	0.0
Filipendula ulmaria	2.2	0.2	0.3	0.0	0.0	0.0	3.8	0.0	0.0	1.7	3.4

Appendix. Continued.

Variable, species	Community type										
	1	2	3	4	5	6	7	8	9	10	11
Galeobdolon luteum	4.9	9.3	0.2	0.0	1.5	0.0	3.4	8.0	3.9	1.4	0.0
Galium aparine	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Galium odoratum	0.0	0.3	1.3	0.0	0.2	0.0	0.0	0.0	1.3	0.1	0.0
Galium uliginosum	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0
Geranium robertianum	0.0	0.0	0.0	0.0	0.0	0.9	0.2	0.0	0.0	2.4	0.0
Mycelis muralis	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.7	0.1	0.0	0.0
Orthilia secunda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0
Oxalis acetosella	0.0	0.5	0.0	0.0	0.0	0.1	3.9	5.9	5.1	0.0	0.0
Paris quadrifolia	0.3	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.2
Poa nemoralis	0.0	0.0	0.7	0.0	1.2	0.0	0.0	0.1	0.1	0.1	0.0
Ranunculus repens	0.4	0.0	0.0	0.0	0.0	0.5	0.0	0.1	0.0	0.0	0.0
Rubus idaeus	0.1	0.0	0.0	0.0	0.2	1.3	0.0	1.2	0.3	0.5	0.0
Rubus saxatilis	0.0	0.0	0.3	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0
Solanum dulcamara	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0
Stellaria holostea	0.5	0.1	0.1	0.0	0.2	0.0	0.1	0.2	0.8	0.0	0.0
Stellaria nemorum	5.0	1.2	0.0	0.0	0.0	0.0	1.8	7.3	0.0	5.6	2.2
Tussilago farfara	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0
Amblystegium serpens	0.2	0.0	0.5	0.0	0.1	0.3	0.4	0.2	0.1	0.4	0.4
Brachythecium reflexum	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Calliergon cordifolium	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0
Calliergonella cuspidata	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.5
Cirriphyllum piliferum	1.6	0.5	0.0	0.0	0.0	0.3	0.4	0.0	0.6	0.0	0.0
Conocephalum conicum	0.1	0.6	0.0	0.0	0.0	2.0	0.0	0.7	0.0	0.3	0.0
Cratoneuron filicinum	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.7	0.0
Eurhynchium hians	12.3	6.4	1.7	9.5	9.8	2.0	0.1	0.6	2.2	3.8	2.5
Pellia endiviifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Plagiochila asplenioides	0.0	0.1	0.0	0.0	0.0	0.0	1.6	0.0	0.4	0.0	0.0
Plagiochila porelloides	0.1	0.1	0.2	0.0	0.5	0.1	0.0	0.0	0.5	0.0	0.0
Plagiomnium affine	0.1	0.0	0.0	0.0	0.0	0.7	1.4	0.0	0.0	0.0	0.0
Plagiomnium cuspidatum	1.1	2.0	0.9	0.3	0.8	0.5	1.8	0.8	0.1	0.5	0.9
Plagiomnium undulatum	1.2	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.0
Pohlia cruda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0