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Vegetation of wetland forests in Latvia: A synopsis

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Using a synsystematical treatment of 625 relevès following the Braun-Blanquet approach, and correspondence (CANOCO) and cluster (TWINSPAN, GROUPAGE) analyses, 13 communities from 3 classes (*Alnetea glutinosae, Querco–Fagetea* and *Vaccinio–Piceetea*) and 7 associations (*Carici elongatae–Alnetum, Sphagno squarrosi–Alnetum, Circaeo–Alnetum, Carici remotae–Fraxinetum, Sphagno girgensohnii–Piceetum, Vaccinio uliginosi–Pinetum* and *Betuletum pubescentis*) are distinguished. A brief overview of the community structure, physiognomical, ecological and phytogeographical features is given.

Key words: boreo-nemoral forest, peatland vegetation, phytosociology, wetland ecology

INTRODUCTION

There is little information available on the community structure of forested wetlands in the northeastern and eastern part of the Baltic region compared with most of Central Europe. In addition, this is a territory where large areas with seminatural wetlands still occur, in contrast to the small patches westwards in Europe. Wetland forests with conifers (*Picea abies, Pinus sylvestris*) are a particular feature (boreal element) of the region. Together with *Alnus glutinosa-, Fraxinus excelsior-, Betula pendula-* and *B. pubescens*-dominated woodlands on swamp peat and wet mineral soil, they form a great variety of well-defined communities. Since forest classification in Fennoscandia and the Baltic States has traditionally followed the forest site-type approach and somewhat different phytosociological principles, difficulties may arise when comparing these vegetation units with the more commonly used syntaxa in Europe that are based on the Braun-Blanquet (1964) approach.

Such a variety of approaches has certainly not contributed to an established and detailed wetland forest syntaxonomy in Europe. This regards both classification issues and a designation of representative samples of community types to be protected, as well as the mapping of vegetation.

Through the present synopsis, I give a brief survey of Latvian wetland forest communities and their site ecology within the frame of the Braun-Blanquet approach.

MATERIAL AND METHODS

Study area

Latvia lies in the boreo–nemoral forest region (Sjörs 1965), on the eastern Baltic coast where both boreal and nemoral

Nomenclature of plants. Tabaka *et al.* (1988) for vascular plants, Düll (in Ellenberg *et al.* 1992) for mosses.

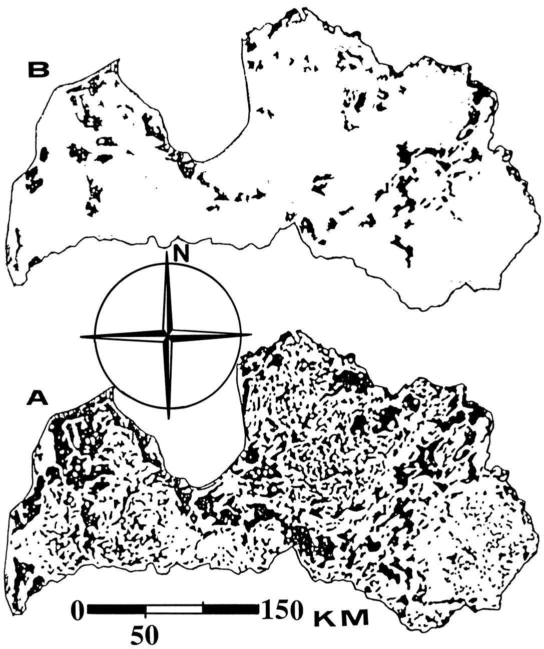

Fig. 1. Forests in Latvia (A, adapted from Encyclopaedia of Latvia, vol. 5-2, GER: Riga, 1984) and the main wetland forests areas (B, original, > 30% of the total forests).

woodlands co-occur. As with some other European countries, the expansion of forest area to former agricultural lands has taken place here — from 24.7% of the total land area in 1923 to more than 40% in the 90s (Anon. 1990). Of the 64.6-thousand-km^2 area, forests occupy ca. 280 thousand km^2, of which around 25% can be classified as wetlands. The principal wetland forest areas are depicted in Fig. 1.

Latvia belongs to the hemiboreal vegetation zone (Ahti *et al.* 1968), where two sections can be distinguished: slightly oceanic (the coastal lowland) and an indifferent one (the other territory). The notable features of the study area are: a relatively mild maritime climate becoming slightly continental towards the inland, precipitation around 600–650 mm annually and a low altitude (40–200 m a.s.l.).

Material

In total, 625 relevès were investigated in 1990–94 (some ecological measurements were completed in 1995). A plot area of 400 m^2 was chosen (600 m^2 for ca. 5% of the plots studied in 1990).

Field studies followed the forest inventory maps (1: 100 000 and 1: 10 000) prepared by the Latvian State Institute for Forest Inventory. All available uniform wetland forest areas of a size not less than 100 ha (also smaller when possible) have been included (Fig. 2).

According to contemporary Latvian forest typology (Bušs 1981), the following wetland forest site types were studied: peatland forests on a peat > 30 cm thick (*Filipendulosa, Dryopterioso-caricosa, Caricoso-phragmitosa, Sphagnosa*) and wet mineral — these include also peatland < 30 cm thick — forests (*Dryopteriosa, Myrtilloso-polytrichosa, Myrtilloso-sphagnosa, Vaccinioso-sphagnosa, Callunoso-sphagnosa*).

The age of the investigated stands fluctuated between 60 and 130 years. Of the 625 relevès, 521 belonged to peatland and 104 to wet mineral forests. Division among the dominant tree species was as follows: *Alnus glutinosa* (150 rels.), *Betula pendula* (134), *Betula pubescens* (82), *Picea abies* (98), *Pinus sylvestris* (142), and *Fraxinus excelsior* (19).

Additionally, 43 relevès from localities studied by other authors (Birkmane 1964, Laivinš 1985, 1989) give supplementary information on the phytosociological structure of Latvian forested wetlands. These were excluded from the summary-type synoptical tables and calculations but are presented in a separate table.

Methods

The synsystematical treatment of data followed the Braun-Blanquet approach (Braun-Blanquet 1964, Westhoff & Van der Maarel 1973, Mueller-Dombois & Ellenberg 1974). Both agglomerative (GROUPAGE) and divisive (TWINSPAN) classification methods were applied. The weighted pair group method and a SR (similarity ratio) resemblance measure were chosen in GROUPAGE. Both hierarchic and indicator division by TWINSPAN were performed with five pseudospecies cut levels (1–5). These corresponded to the Braun-Blanquet cover-abundance scale (exception: indices "r", "+", and "1" were treated as one cut level), which was applied as follows: r (1–3 individuals), + (few individuals), 1 (< 5%), 2 (5.1–25%), 3 (25.1–50%), 4 (50.1–75%), and 5 (75.1–100%). In synoptical tables, the frequency "r" means less than 5% and the other frequency classes represent the following percentage intervals: I (5–20%), II (20.1–40%), III (40.1–60%), IV (60.1–80%), and V (80.1–100%).

The program DCA (Detrended Reciprocal Averaging) from the CANOCO package was used to ordinate plots and species. The default options of the computing programs were chosen. When DCA-ordination was performed, no samples or species were omitted, species (sample)-weights specified or rare species downweighted. Details of the algorithm used in the programs, as well as a comprehensive explanation, can be found in Hill (1979), Gauch (1982), Jongman *et al.* (1987), and Ter Braak (1990).

Phytogeographical analyses and indicator values for soil reaction, moisture, light and soil fertility (nitrogen) were calculated, weighted by coverage, and by taking the species with frequency above 5% into consideration. The initial data for these calculations were taken from Meusel *et al.* (1965, 1978, 1992), Hultèn and Fries (1986), Fatare (1989), Ellenberg *et al.* (1992) for phytogeographical analy-

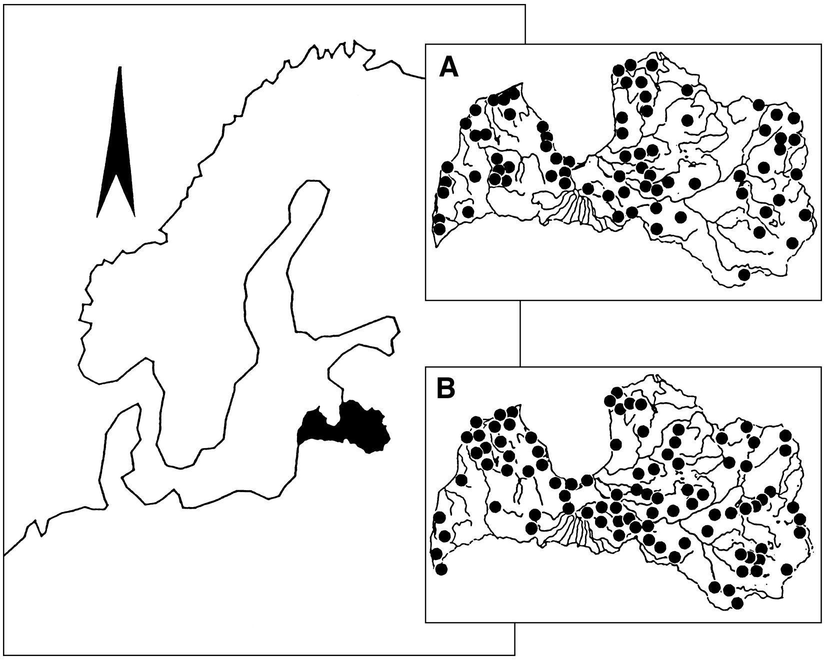

Fig. 2. Geographical position of Latvia and the study areas of wet mineral (A) and peatland (B) forests.

ses and Ellenberg *et al.* (1992) for indices representing the site ecology.

The depth of the groundwater level was measured in the centre of a plot (point of intersection of diagonals of a 20 × 20-m plot). The same applies to the measurements of the peat layer. The height of the tree layer was measured in 80–100-year-old stands with a Blume-Leiss height-meter.

DBH (diameter at breast height) of trees was measured on a 20 × 20-m plot (except shrub-like species as *Sorbus aucuparia*) and DBH classes were divided as follows: I = < 10 cm, II = 10.1–20 cm, III = 20.1–30 cm, IV = 30.1–40 cm, V = > 40.1 cm (finally expressed as a percentage of the total number of trees). Only 80–100-year-old stands were included and those with crown closure not deviating more than 10% from the mean figure, characterising the community in Latvia on the whole.

It should be noted that some of the summarised data (e.g. lists of single plots, seasonal fluctuation of water level, etc.) can be found in detail in papers on phytogeography, alder peatlands, pine–birch bogs, etc. (Prieditis 1993a–d, 1997ab). The number of species included in the ordination procedure of all 13 Latvian wetland forest communities (based on summarised synoptical tables) by DCA (Figs. 4 and 5) was restricted to those present in at least 3 communities (frequency class not lower than II; high frequency species-classes III, IV and V were included without any limitation), but for the GROUPAGE analysis (Fig. 6), with frequency-class II in at least one community. Species with the first frequency class were only included in the analysis if they were present in at least 5 communities. Only the most essential references from other territories have been cited (summary on the syntaxa, description of a new syntaxon or approach, etc.).

DESCRIPTION OF THE SYNTAXA

General

In total, 347 vascular plant and moss species have been found in Latvian wetland forests. Of these, 66 are occasional (recorded in 1 or 2 relevès from 625). A simplified classification for the first divisions by TWINSPAN is given (Fig. 3). The floristical structure of wetland forests in Latvia coincides well with similar assemblages studied in Lithuania (Baleviciene 1991) and Estonia (Rühl 1936).

Although comparison with the forest site-type approach is beyond the scope of the present paper, it should be noted that the distinguished syntaxa are poorly correlated with the site-type classification units, particularly within the fertile and rich wetland forests. Also, the evidence of a peat layer does not point at the intrinsic importance of a phytosociological differentiation between communities belonging to different forest site-types (e.g. *Sphagno girgensohnii–Piceetum* (> 30 cm peat) belongs to *Dryopterioso-caricosa* site-type, but *Sphagno girgensohnii–Piceetum* (< 30 cm peat) belongs to *Myrtilloso-polytrichosa* site-type).

Consequently, the following syntaxonomical structure of Latvian wetland forests can be estab-

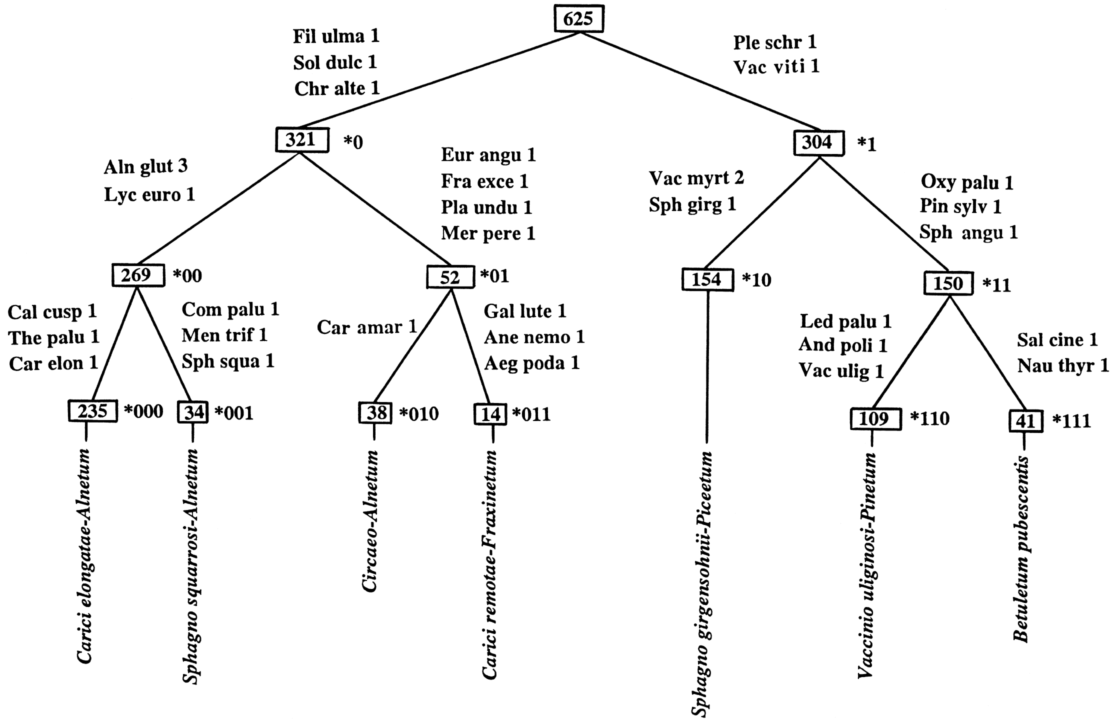

Fig. 3. Two-way indicator species analysis (TWINSPAN) for the first divisions of the classification (see Appendix for the abbreviations).

lished (13 syntaxa in 3 classes with 7 associations):

Cl. *Alnetea glutinosae* Br.-Bl. et Tx. 1943
O. *Alnetalia glutinosae* Tx. 1937 em. Oberd. 1953
All. *Alnion glutinosae* (Malc. 1929) Meijer Drees 1936 em. Th. Müll. et Görs 1958
Ass. *Carici elongatae–Alnetum* Schwick. 1933
Subass. *C.e.–A. typicum* Meijer Drees 1936
Subass. *C.e.–A. cardaminetosum* Meijer Drees 1936
Ass. *Sphagno squarrosi–Alnetum* Sol.-Gorn. ex Pried. 1997

Cl. *Querco–Fagetea* Br.-Bl. et Vlieg. in Vlieg. 1937 em. Klika 1939
O. *Fagetalia sylvaticae* Pawl. 1928
All. *Alno–Ulmion* Br.-Bl. et Tx. ex Tchou 1948 em. Th. Müll. et Görs 1958
SubAll. *Alnenion glutinoso-incanae* Oberd. 1953
Ass. *Circaeo–Alnetum* Oberd. 1953
(syn. Ass. *Fraxino–Alnetum glutinosae* Matuszk. 1952)
Ass. *Carici remotae–Fraxinetum* Koch ex Faber 1936

Cl. *Vaccinio–Piceetea* Br.-Bl. 1939
O. *Vaccinio–Piceetalia* Br.-Bl. 1939
All. *Dicrano–Pinion* Libb. 1933
Ass. *Betuletum pubescentis* (Hueck 1929) Tx. 1937 em. Tx. 1955
Ass. *Vaccinio uliginosi–Pinetum sylvestris* (Hueck 1925) Kleist 1929
Subass. *V.u.–P. molinietosum* Czerw. 1970
Subass. *V.u.–P. typicum* Czerw. 1970
V.u.–P.t. variant with *Phragmites australis*
V.u.–P.t. variant with *Calluna vulgaris*
All. *Vaccinio–Piceion* Br.-Bl., Sissingh et Vlieger 1939 em. K-Lund 1967
Ass. *Sphagno girgensohnii–Piceetum* (Br.-Bl. 1939) Polak. 1962
S.g.–P. variant with *Crepis paludosa*
Subass. *S.g.–P. myrtilletosum* Polak. 1962
S.g.–P.m. variant with *Pinus sylvestris.*

Communities of Eurosiberian alder swamps (Cl. *Alnetea glutinosae*)

This is a woodland type occupying a very distinctive suite of primary habitats: from rich, swampy sites and fens to places where there is a tendency for paludification and intensive accumulation of *Sphagnum* peat.

Three communities from 2 associations (*Carici elongatae–Alnetum* and *Sphagno squarrosi–Alnetum*) can be distinguished (Table 1). The canopy is characterised by the high frequency and abundance of *Alnus glutinosa*, in some places also of *Betula pendula, B. pubescens* and *Fraxinus excelsior* (the latter only in fertile habitats).

Carici elongatae–Alnetum is quite a complex community, which has lately been divided into 2–3 subassociations (Döring-Mederake 1990, 1991, Prieditis 1997a). *Alnus glutinosa, Salix cinerea, S. aurita, Frangula alnus, Ribes nigrum, Solanum dulcamara, Lycopus europaeus, Lysimachia vulgaris, Thelypteris palustris, Carex elongata* and *Calliergonella cuspidata* are good character species of the alderwoods in the Baltic region and northern-central Europe (Matuszkiewicz 1984ab, Baleviciene 1991, Döring-Mederake 1991). This concept has changed little since the classic prodromal synopsis compiled by Bodeux (1955).

A high variability of the internal structure of *Carici elongatae–Alnetum typicum* can be expected. It occupies floodplains of rivers and lakes, places with underground water outflow (including sites with both standing water and a surface run-off), and temporarily flooded habitats with moving subsoil streams. Hence the floristic structure and the nutrient status may strongly fluctuate from place to place.

Compared with the previous concept on Latvian alderwoods (Prieditis 1993b), the names of subassociations within *Carici elongatae–Alnetum*

Table 1. The community structure of Latvian forested wetlands belonging to *Alnetea glutinosae*; with the frequency class and mean cover-abundance of species (a: *Carici elongatae-Alnetum typicum*, b: *C.e.-A.cardaminetosum*, c: *Sphagno squarrosi-Alnetum*; * = cover-abundance indicated also for *Betula*- or *Fraxinus*-dominated stands).

	a	b	c
Tree layer (mean %)	90	95	85
Shrub layer (mean %)	50	30	50
Herb layer (mean %)	90	90	65
Moss layer (mean %)	20	25	50
Number of plots studied	198	37	34
Species (mean per plot)	30.0	29.5	26.2
Diagnostic species of Cl, O, All, Ass, sAss			
Alnus glutinosa	V.5	V.5	V.5
Frangula alnus	IV.2	III.1	III.1
Salix cinerea	I.1	I.1	I.1
Solanum dulcamara	IV.2	V.1	IV.1
Lycopus europaeus	IV.1	IV.1	III.1
Lysimachia vulgaris	V.1	III.1	IV.1
Galium palustre	V.1	V.1	V.1
Thelypteris palustris	IV.1	II.1	II.1
Carex elongata	IV.1	III.1	I.1
Calliergonella cuspidata	III.1	II.2	I.1
Ribes nigrum	II.1	II.1	–
Carex elata	II.1	–	I.+
Urtica dioica	II.1	IV.3	I.1
Ranunculus repens	II.1	IV.2	I.1
Cardamine amara	II.1	II.1	I.1
Malachium aquaticum	I.1	III.2	–
Athyrium filix-femina	II.1	IV.2	I.1
Chrysosplenium alternifolium	II.1	IV.2	–
Sphagnum squarrosum	I.1	I.1	IV.2
Vaccinium myrtillus	I.1	I.+	III.2
Carex canescens	I.1	I.1	III.1
Comarum palustre	I.1	I.1	IV.2
Pleurozium schreberi	I.1	I.1	III.2
Menyanthes trifoliata	I.1	–	III.2
Calla palustris	I.1	I.1	III.3
Peucedanum palustre	II.1	I.1	IV.1
Carex vesicaria	I.1	–	II.1
Sphagnum palustre	I.1	–	II.1
Sphagnum teres	I.+	–	II.1
Other species			
Filipendula ulmaria	IV.2	III.2	III.1
Geum rivale	III.1	II.1	r.1
Naumburgia thyrsiflora	III.1	III.1	IV.1
*Betula pendula**	IV.2(5)	V.1(5)	IV.1(5)
Picea abies	IV.1	IV.1	II.1
*Betula pubescens**	I.1(5)	I.1(5)	I.1(5)
*Fraxinus excelsior**	II.1(5)	I.1(5)	–
Sorbus aucuparia	III.1	II.1	II.1
Glyceria fluitans	II.1	I.1	I.1
Equisetum palustre	II.1	I.1	I.1
Climacium dendroides	III.1	I.1	I.1
Crepis paludosa	II.1	II.1	–
Cirsium oleraceum	II.1	III.1	–
Oxalis acetosella	II.1	III.1	I.1
Deschampsia caespitosa	II.1	III.1	III.1
Angelica sylvestris	II.1	III.1	I.1
Viola palustris	III.1	II.1	III.1
Myosotis palustris	II.1	I.1	–
Plagiomnium ellipticum	II.1	III.1	II.1
Padus avium	I.1	II.1	I.1
Caltha palustris	II.1	I.1	II.1
Impatiens noli-tangere	I.1	II.1	–
Iris pseudacorus	II.1	–	II.1
Carex acutiformis	II.2	–	r.1
Scirpus sylvaticus	II.2	II.1	II.1
Phragmites australis	II.1	–	I.1
Pseudobryum cinclidioides	II.1	I.1	–
Equisetum fluviatile	II.1	–	III.1
Juncus effusus	II.1	II.1	II.1
Dryopteris carthusiana	II.1	III.1	II.1
Cirriphyllum piliferum	II.1	II.1	I.1
Dicranum polysetum	r.1	r.1	II.1

have been adjusted (since these are synonyms) to the earlier valid concept developed by Döring-Mederake (1990, 1991). Thus, Latvian *Carici elongatae–Alnetum typicum, C.e.–A. thelypteridetosum, C.e.–A. caricetosum elatae* (Prieditis 1993b) have been identified as *Carici elongatae–Alnetum typicum* Meijer Drees 36, but *C.e.–A. urticetosum* (Möller 70) Pried. 93 as *Carici elongatae–Alnetum cardaminetosum* Meijer Drees 36. Due to the strong resemblance in terms of floristic features and site ecology with central European *C.e.–Alnetum typicum*, the communities with *Thelypteris palustris* and *Pseudobryum cinclidioides* or tall sedges (*Carex acutiformis, C. elata*) in Latvia have now been included into the typical subassociation and have to be understood in a wider sense. If one wishes, these may be separated still at the level of a variant.

Carici elongatae–Alnetum cardaminetosum has a more uniform ecological and physiognomical suite. It occupies comparatively richer sites on fen peat, usually in extremely marshy habitats rich in streams or moving water close to the ground surface. *Chrysosplenium alternifolium, Urtica dioica* and *Ranunculus repens* are quite abundant and are confined to these richer alderwoods. *Athyrium filix-femina* and *Malachium aquaticum,* tolerating somewhat wetter conditions, have also been recorded in large quantities.

A detailed analysis of Central-, North- and East-European lowland alderwoods has supported the establishment of a separate *Sphagno squarrosi–Alnetum* association (Solinska-Gornicka 1987, Prieditis 1997a). These assemblages are better represented by many species generally not confined to *Alnion*, but frequent in *Vaccinio–Piceetea, Phragmitetea, Scheuchzerio–Caricetea fuscae* and even *Oxycocco–Sphagnetea*. Although such compositions have sometimes been ascribed (e.g. Döring-Mederake 1990, 1991) to *Carici elongatae–Alnetum betuletosum* (or *C.e.–A. sphagnetosum*), there is a clear difference to be found both in site ecology and species composition from the other subassociations belonging to *Carici elongatae–Alnetum*. The vicinities of bogs and mires, with a tendency to paludification, are typical habitats for *Sphagno squarrosi–Alnetum*. Baleviciene (1991) points out its syntaxonomical closeness to *Vaccinio–Piceetea.* The absence of groundwater movement and a highly water-saturated substrate leads to low pH and oligotrophic-growth conditions. Among *Sphagnum squarrosum, Vaccinium myrtillus, Carex canescens, Menyanthes trifoliata* and *Calla palustris*, the following mire species also belong to the commoner field-layer associates: *Carex vesicaria, Comarum palustre, Equisetum fluviatile* and, locally, *Carex rostrata*.

All the communities of *Alnetea glutinosae* are quite widespread throughout the country.

Communities of wetland European broad-leaved forests (Cl. *Querco–Fagetea*)

Only two communities at the level of association (*Circaeo–Alnetum* and *Carici remotae–Fraxinetum*) can be distinguished in Latvia (Table 2), predominated by *Alnus glutinosa, Fraxinus excelsior, Betula pendula,* and rarely by *B. pubescens* in the tree layer. As with *Alnetea glutinosae* communities, here *Betula* sp. often reaches high abundances. Although some authors point out that the birch wetlands have to be synsystematically separated as a variant (e.g. Patalauskaite 1991) or a distinct association (e.g. Czerwiński 1972), the applied classification and ordination techniques in this study do not support such an approach. Neither the floristical structure nor site ecology of birch-dominated stands deviate significantly from the commoner compositions of a wetland community dominated either by *Alnus glutinosa* or *Fraxinus excelsior*.

The *Circaeo–Alnetum* forest lies mostly on a poorly-decomposed layer of organic deposits or medium-decomposed woody–herbaceous peat, with loamy sand within the reach of trees. In Latvia, this community occupies small areas on slightly elevated slopes or at brooks. A mosaic pattern and elevated hummocks are also important physiognomical features of such a woodland. The streams support a good nutrient circulation, especially after heavy rains. Several *Alno–Ulmion* character species, such as *Mercurialis perennis, Crepis paludosa, Malachium aquaticum, Chrysosplenium alternifolium,* as well as the bryophytes *Plagiomnium undulatum* and *Eurhynchium angustirete,* are the most common plants in the field level. To summarize, meso–eutrophic and eutrophic plants predominate among the field-layer species. The moss-layer species are rather variable in their total cover but their distribution is patchy and runs from the wetter to the drier nano-relief. However, only very few bryophytes reach the second frequency class.

The *Carici remotae–Fraxinetum* woodland is the only Latvian wetland forest where a distinct vernal and summer (autumn) aspect can be distinguished. *Anemone nemorosa, Ranunculus cassubicus, Galeobdolon luteum* and *Mercurialis perennis,* sometimes accompanied by abundantly blooming *Lonicera xylosteum,* form a virtually continuous and very prominent cover in May and are associated in places also with *Viola mirabilis, Lathyrus vernus* and *Pulmonaria obscura*. In the summer aspect, taller herbs such as *Aegopodium podagraria, Filipendula ulmaria, Crepis paludosa* and *Cirsium oleraceum* predominate.

Compared with *Circaeo–Alnetum, Carici remotae–Fraxinetum* is mostly a wet soil community on gleyey soils without evident peat accumulation. It occupies small patches on gentle slopes, habitats rich in cold springs and well-drained sites at the riverside or at fast-flowing streams. Long strips of deposited silt can also be found after a flood-flush. In Latvia, the distribution of *Carici remotae–Fraxinetum* and *Circaeo–Alnetum* is particularly uneven, mostly coinciding with the areas under primarily broad-leaved forests (Sakss 1955). Within a contemporary syntaxonomical frame, designated for such wetlands in Europe (Neuhäuslova-Novotna 1977, Matuszkiewicz 1984b, Döring-Mederake 1991, Wittig & Dinter 1991, Härdtle 1995), no distinct subassociations are recognized in Latvia, although the compositions of *Carici remotae–Fraxinetum* quite unambiguously refer to *C.r.–F. typicum* Knapp (44)48.

Table 2. The community structure of Latvian forested wetlands belonging to *Querco–Fagetea*; with the frequency class and mean cover-abundance of species (a: *Circaeo–Alnetum*, b: *Carici remotae–Fraxinetum*; * = cover-abundance indicated also for *Betula*-dominated stands).

	a	b
Tree layer (mean %)	90	90
Shrub layer (mean %)	30	60
Herb layer (mean %)	80	80
Moss layer (mean %)	30	35
Number of plots studied	38	14
Species (mean per plot)	32.7	33.9
Diagnostic species of Cl, O, All, Ass		
Fraxinus excelsior	IV.2	V.5
Alnus glutinosa	V.5	V.1
Plagiomnium undulatum	III.2	III.2
Mercurialis perennis	III.2	IV.3
Eurhynchium angustirete	III.2	III.1
Padus avium	III.1	III.2
Crepis paludosa	III.3	IV.1
Equisetum sylvaticum	III.1	III.1
Malachium aquaticum	IV.3	III.1
Chrysosplenium alternifolium	III.2	III.1
Cardamine amara	III.1	I.1
Aegopodium podagraria	II.1	IV.1
Galeobdolon luteum	I.+	IV.1
Carex remota	II.1	III.1
Anemone nemorosa	I.1	IV.1
Lonicera xylosteum	r.1	III.1
Carex sylvatica	–	III.1
Ranunculus cassubicus	–	III.1
Other species		
Betula pendula (et *B. pubescens*)*	V.2(5)	II.1(5)
Picea abies	IV.1	V.1
Geum rivale	IV.2	IV.1
Dryopteris carthusiana	IV.1	III.1
Oxalis acetosella	III.1	IV.1
Filipendula ulmaria	III.2	III.2
Ranunculus repens	III.2	III.1
Galium palustre	III.1	III.1
Cirsium oleraceum	III.1	III.1
Urtica dioica	III.1	II.1
Rubus idaeus	III.1	II.1
Angelica sylvestris	III.1	II.1
Deschampsia caespitosa	II.1	III.1
Tilia cordata	I.+	III.1
Caltha palustris	I.1	III.1
Acer platanoides	I.1	III.1
Ulmus glabra	I.+	III.1
Equisetum palustre	III.1	r.1
Frangula alnus	II.2	II.1
Climacium dendroides	II.1	II.1
Cirriphyllum piliferum	II.1	II.1
Brachythecium curtum	II.1	II.1
Daphne mezereum	II.1	II.1
Impatiens noli-tangere	II.2	I.1
Lysimachia vulgaris	II.1	I.1
Sorbus aucuparia	I.1	II.1
Athyrium filix-femina	II.1	–
Scirpus sylvaticus	II.1	–
Juncus effusus	II.1	–
Viola mirabilis	–	II.1
Rhodobryum roseum	–	II.1

Communities of boreal coniferous forests. Pine and pine–birch wetlands (*Vaccinio–Piceetea, Dicrano–Pinion*)

These assemblages represent forested bogs and transitional mires (Table 3), belonging to 5 communities from 2 associations (*Vaccinio uliginosi–Pinetum* and *Betuletum pubescentis*).

Vaccinio uliginosi–Pinetum is a typical forest bog community where *Pinus sylvestris* and *Oxycocco–Sphagnetea* species predominate. Following the investigations by Sokołowski (1966b) and Czerwiński (1970), these communities may be divided into two subassociations: *typicum* and *molinietosum*. The first one (*typicum*, called also *V.u.–P. sphagnetosum* in Sokołowski (1980), however this cannot be accepted as the legitime epithet (art. 5, 29 of the Code), as the priority belongs to *V.u.–P. typicum* Czerw. 70) is the most widespread deep peatland forest community in Latvia, poor in species and uniform throughout the country. *Vaccinium uliginosum, Eriophorum vaginatum, Oxycoccus palustris, Ledum palustre, Sphagnum magellanicum* and *S. angustifolium* are highly abundant on almost every relevè.

Vaccinio uliginosi–Pinetum molinietosum and *V.u.–P. typicum* var. *Calluna vulgaris* are mostly distributed in western Latvia within the coastal lowland. Both are mineral–wet-soil communities with a thin, poorly decomposed peat layer in some sites.

Although a very similar community, *Vaccinio myrtilli–Pinetum molinietosum* Sokol. 66 (Sokołowski 1966b) has been recognized in Poland (and also *Molinio–Pinetum* ass. prov. (Matuszkiewicz 1984 b)), I found that the character species of *Dicrano–Pinion* and *Oxycocco–Sphagnetea* are still equally represented in *Vaccinio uliginosi–Pinetum molinietosum* and this has more resemblance in site ecology to *Vaccinio uliginosi–Pinetum* than to the typical dryland pine forests grouped around *Vaccinio myrtilli–Pinetum*.

Vaccinio uliginosi–Pinetum molinietosum represents a sparse pine–spruce woodland with an open understorey and scrubby patches consisting of *Myrica gale*. *Vaccinium uliginosum, V. myrtillus, V. vitis-idaea* and *Molinia caerulea* are the most abundant species in the field layer.

In the coastal lowland, the acid-mineral wet soils, which are extremely poor in nutrients, are occupied by *Vaccinio uliginosi–Pinetum typicum* var. *Calluna vulgaris*. Considerable enrichment of the moss layer with some *Sphagna*, such as *S. capillifolium, S. cuspidatum* and *S. rubellum* can be noted in addition to the species characterizing the *V.u.–P. typicum* forested bogs.

In order to follow a unified approach to the Latvian wetland forests, the subass. prov. *Vaccinio uliginosi–Pinetum phragmitetosum* (Prieditis 1993a) has been altered into a variant under the typical subassociation. This decision is due to the lack of principal differences in site ecology as compared with *V.u.–P. typicum.* Although there is an indication towards the mesotrophic assemblages (decrease in *Oxycocco–Sphagnetea*, but increase in *Scheuchzerio–Caricetea fuscae (nigrae)* and *Alnetea glutinosae* species), this does not represent any floristically and ecologically distinct community (subassociation) and is, in fact, a fertile variant of forest bogs in deep peat. As well as

Table 3. The community structure of Latvian forested wetlands belonging to *Vaccinio–Piceetea*, *Dicrano–Pinion*; with the frequency class and mean cover-abundance of species (a: *Vaccinio uliginosi–Pinetum molinietosum*, b: *Vaccinio uliginosi–Pinetum typicum*, c: *V.u.–P. typicum* var. *Calluna vulgaris*, d: *V.u.–P. typicum* var. *Phragmites australis*, e: *Betuletum pubescentis*; * = frequency class and cover-abundance indicated also for *Pinus*- or *Betula pubescens*-dominated stands).

	a	b	c	d	e
Tree layer (mean %)	65	70	70	75	75
Shrub layer (mean %)	25	20	15	40	40
Herb layer (mean %)	70	80	70	80	80
Moss layer (mean %)	70	95	90	80	65
Number of plots studied	10	44	8	47	41
Species (mean per plot)	19.7	18.8	16.8	24.5	35.8

(Continues …)

Table 3. Continued.

Diagnostic species of Cl, O, All, Ass, sAss					
*Pinus sylvestris**	V.5	V.5	V.5	V.5	III.1(V.5)
Polytrichum commune	III.1	IV.3	III.1	III.2	III.2
Oxycoccus palustris	III.1	V.3	IV.1	III.2	III.2
Vaccinium uliginosum	IV.2	V.2	V.4	IV.2	II.1
Eriophorum vaginatum	I.1	V.4	V.2	III.2	II.2
Ledum palustre	I.1	V.4	III.2	III.2	I.1
Sphagnum magellanicum	I.1	V.3	V.4	II.3	II.2
Andromeda polifolia	I.1	IV.2	IV.2	II.2	II.1
Sphagnum angustifolium	II.1	IV.3	V.3	II.2	I.2
Pleurozium schreberi	V.3	IV.2	II.1	III.1	II.1
Vaccinium vitis-idaea	V.2	III.1	II.1	III.1	II.1
Picea abies	V.3	IV.1	I.1	IV.1	IV.2
Vaccinium myrtillus	V.2	–	I.+	I.+	I.+
Molinia caerulea	IV.1	I.1	I.+	I.1	II.2
Myrica gale	IV.1	–	–	–	r.1
Betula pendula	–	II.1	–	III.1	III.1
*Betula pubescens**	III.1	II.1	II.1	III.1	III.3(V.4)
Frangula alnus	I.1	II.1	I.1	III.2	IV.2
Salix cinerea	I.1	I.1	–	II.1	IV.2
Peucedanum palustre	II.+	I.1	–	II.1	IV.2
Galium palustre	I.1	I.1	I.1	II.1	IV.1
Calamagrostis canescens	II.1	r.1	–	II.1	III.1
Filipendula ulmaria	I.+	–	–	I.1	III.1
Naumburgia thyrsiflora	–	–	–	I.1	III.1
Thelypteris palustris	–	–	–	I.1	III.2
Menyanthes trifoliata	I.1	I.1	I.1	II.1	III.2
Comarum palustre	I.1	I.1	I.1	II.1	III.2
Diagnostic species of the variant					
Sphagnum capillifolium	II.1	III.2	IV.1	II.1	r.1
Sphagnum rubellum	I.1	III.1	V.1	I.1	r.1
Sphagnum cuspidatum	I.1	I.1	IV.1	I.1	r.1
Calluna vulgaris	II.1	III.1	V.3	II.1	r.1
Phragmites australis	II.1	I.1	I.1	V.3	II.2
Carex echinata	I.1	I.1	I.1	III.2	II.2
Carex nigra	I.1	II.1	I.1	III.2	III.1
Alnus glutinosa	–	–	–	II.2	II.2
Salix aurita	I.1	r.1	–	II.1	I.1
Sphagnum warnstorfii	II.1	I.1	I.1	II.2	I.1
Potentilla erecta	I.1	–	I.+	II.2	II.2
Other species					
Melampyrum pratense	IV.1	IV.1	II.1	III.1	II.1
Carex elongata	–	–	–	I.1	II.1
Calliergonella cuspidata	–	–	–	I.1	II.1
Empetrum nigrum	II.2	III.2	II.1	I.1	I.1
Drosera rotundifolia	I.1	II.+	I.1	I.1	I.1
Rubus chamaemorus	I.1	II.3	II.1	I.3	–
Pyrola rotundifolia	–	–	–	I.1	II.1
Luzula pilosa	I.1	–	–	I.1	II.1
Lysimachia vulgaris	I.1	–	–	II.1	II.1
Angelica sylvestris	I.+	–	–	I.+	II.+
Carex rostrata	III.1	r.+	–	I.1	I.2

V.u.–P. typicum, the variant with *Phragmites australis* is widespread throughout the country.

The *Betuletum pubescentis* association is rich in species and occurs scattered in the coastal lowland and around inland lakes (Tüxen 1955). This association represents transitional mires on medium–deep peatland, rich in underground streams and base-rich deeper horizons. Complicate assemblages of species (usually without any dominant) from the *Vaccinio–Piceetea, Phragmitetea, Alnetea glutinosae, Scheuchzerio–Caricetea fuscae* and *Oxycocco–Sphagnetea* classes co-occur there.

Communities of boreal coniferous forests. Spruce wetlands (*Vaccinio–Piceetea, Vaccinio–Piceion*)

In Latvia, these forested wetlands are represented by 3 communities, all belonging to the association *Sphagno girgensohnii–Piceetum* (Table 4). This is a syntaxon marking well the distribution of boreo–nemoral and southern boreal spruce wetlands within the lowland area of *Picea abies* in Europe — from eastern Poland and Fennoscandia towards the Urals (Polakowski 1962, Sokołowski 1966a, Vassilevitch 1983). Although some alternative suggestions on the synsystematical position of *Sphagno girgensohnii–Piceetum* have been published (incl. new suball. *Sphagno–Piceion sensu* Endler), the community is still placed under *Vaccinio–Piceion* (Braun-Blanquet *et al.* 1939).

Following the original diagnosis (Polakowski 1962), *Sphagno girgensohnii–Piceetum* is a primary spruce forest on wet, peaty (up to 1.5 m thick) soil of a mesotrophic character (differential species: *Picea abies, Lycopodium annotinum, Sphagnum girgensohnii, Trientalis europaea, Corallorhiza trifida, Listera cordata*).

Table 4. The community structure of Latvian forested wetlands belonging to *Vaccinio–Piceetea*, *Vaccinio–Piceion*; with the frequency class and mean cover-abundance of species (a: *Sphagno girgensohnii–Piceetum* var. *Crepis paludosa*, b: *S.g.–P. myrtilletosum*, c: *S.g.–P. myrtilletosum* var. *Pinus sylvestris*).

	a	b	c
Tree layer (mean %)	80	80	70
Shrub layer (mean %)	40	50	20
Herb layer (mean %)	80	70	60
Moss layer (mean %)	60	50	80
Number of plots studied	69	74	11
Species (mean per plot)	30.1	31.0	28.4
Diagnostic species of Cl, O, All, Ass			
Picea abies	V.4	V.5	V.3
Oxalis acetosella	V.1	III.1	I.1
Maianthemum bifolium	III.1	IV.1	II.+
Hylocomium splendens	III.1	III.2	III.2
Sphagnum girgensohnii	II.2	V.2	I.1
Vaccinium myrtillus	II.1	V.1	II.1
Comarum palustre	I.1	III.2	I.1
Vaccinium vitis-idaea	I.+	III.1	III.2
Pleurozium schreberi	II.1	III.1	III.1
Rhytidiadelphus triquetrus	II.1	III.1	III.2
Luzula pilosa	II.+	III.1	IV.1
Diagnostic species of the variant			
Cirsium oleraceum	IV.2	I.1	II.+
Geum rivale	IV.2	I.+	–
Crepis paludosa	IV.1	II.1	I.+
Athyrium filix-femina	III.1	I.+	–
Ranunculus repens	III.1	I.+	I.+
Plagiomnium ellipticum	III.1	I.1	I.+
Filipendula ulmaria	III.1	I.1	III.1
Pinus sylvestris	II.1	II.1	V.4
Sphagnum capillifolium	–	I.1	III.1
Betula pubescens	II.1	II.1	IV.+
Anemone nemorosa	I.1	–	III.1
Other species			
Dryopteris carthusiana	IV.1	III.1	III.+
Sorbus aucuparia	III.1	III.1	III.+
Lysimachia vulgaris	III.2	III.1	III.1
Calamagrostis canescens	III.1	III.1	III.1
Galium palustre	III.1	III.1	III.+
Frangula alnus	IV.1	IV.1	II.1
Betula pendula	IV.1	IV.2	I.+
Viola palustris	III.1	III.+	II.+
Deschampsia caespitosa	III.1	II.1	II.+
Alnus glutinosa	III.1	II.1	III.+
Carex nigra	II.1	III.1	II.1
Trientalis europaea	II.1	II.1	III.+
Calamagrostis neglecta	II.+	II.1	II.1
Caltha palustris	II.1	II.+	II.+
Rubus idaeus	II.1	II.1	I.1
Peucedanum palustre	I.1	II.1	II.+
Naumburgia thyrsiflora	I.1	II.1	I.+
Orthilia secunda	I.+	II.1	II.+
Dicranum polysetum	I.+	II.1	III.+
Sphagnum palustre	I.+	II.1	II.1
Climacium dendroides	II.1	I.+	II.1
Plagiomnium cuspidatum	II.1	I.+	I.1
Carex elongata	II.1	I.1	I.+
Thelypteris palustris	II.1	I.1	I.+
Polytrichum commune	–	I.+	II.1

From the three recognized subassociations (… *lycopodietosum, … myrtilletosum, … dryopteridetosum*), only *S.g.–P. myrtilletosum* can be distinguished in Latvia. It has a well-developed stratum consisting of 4 layers and a mosaic pattern of herbs and mosses. Usually, no dominating herb-layer species can be distinguished. Often, there is considerable enrichment of the ground cover by *Vaccinio–Piceion* character species, such as *Oxalis acetosella, Maianthemum bifolium, Vaccinium vitis-idaea, V. myrtillus, Sphagnum girgensohnii, Rhytidiadelphus triquetrus* and *Hylocomium splendens*. On the other hand, species confined to wet broad-leaved forests are very rare.

The variant in fertile soils (*S.g.–Piceetum* var. *Crepis paludosa*) has a clearer resemblance to alderwoods. This is expressed both in site ecology (hummocky habitats, outflowing streams) and the floristic set (decrease in *Vaccinio–Piceion* species in favour of the rich *Alnion* species). Thus, edaphic variation plays an important role in the forming of the physiognomical suite of the variant. However, it cannot be excluded that this community has been affected by minor silvicultural treatment because, by the late 80s, deciduous wetlands (e.g. alderwoods) were replaced with spruce monocultures when clear-cutting became a common practice in Latvia.

The third community is quite specific: *S.g.–P. myrtilletosum* var. *Pinus sylvestris* where both *Picea abies* and *Pinus sylvestris* can be equally found in the tree layer with scattered *Betula pubescens* in admixture. A very restricted set of species, a comparatively sparser tree-, shrub- and herb-layer and a dense moss layer (mostly *Hylocomium splendens* and *Rhytidiadelphus triquetrus* associated by *Polytrichum commune, Sphagnum capillifolium, S. girgensohnii* and *S. palustre*) can be recognized. This community is also characterised by a thin, poorly-decomposed peat layer.

In Latvia, most of the spruce wetlands are restricted to the northern part of the country, especially to the north-easternmost districts.

Sokołowski (1980) has published a variety of invalid names of wet spruce forest associations, hardly distinguishable on a wider (European) scale, with *Sphagno girgensohnii–Piceetum* in particular. These syntaxa are *Vaccinio myrtilli–Piceetum* nom. inval., *Betulo pubescentis–Piceetum* nom. inval. and *Piceo-Alnetum* nom. inval. (art. 5 of the Code (Barkman *et al.* 1986)). Although in Latvia *Sphagno girgensohnii–Piceetum* var. *Crepis paludosa* has some resemblance to *Betulo pubescentis–Piceetum* nom. inval., the applied processing of Latvian data (Prieditis 1993d, 1997b) did not enable the separation of the designated character species as strictly as claimed by Sokołowski (1980) and Baleviciene (1991).

Other investigations in Latvian forested wetlands

A brief survey on the other studies in Latvian wetland forests is given in Table 5.

Physiognomical, ecological and phytogeographical features

Important features characterising particular aspects of the physiognomical suite, site ecology and the geographical variation of species are summarised in Table 6.

Clear differences among the communities can be recognized in all presented characters. In sum-

Table 5. Phytosociological studies in Latvian wetland forests by the other authors.

Source	Dominant	Locality	Plots	Community *sensu* present paper
Laivinš 1989	*Alnus glutinosa*	Pahatnieki & Pilori	8	*Carici elongatae–Alnetum typicum*
Laivinš 1985	*Alnus glutinosa*	Latvian lake islands	11	*Carici elongatae–Alnetum typicum*
Laivinš 1985	*Alnus glutinosa*	Latvian lake islands	9	*Sphagno squarrosi–Alnetum*
Birkmane 1964	*Alnus glutinosa*	Kraslava (E Latvia)	4	*Carici elongatae–Alnetum typicum*
Birkmane 1964	*Betula* sp.	Kraslava (E Latvia)	5	*Carici elongatae–Alnetum typicum*
Birkmane 1964	*Pinus sylvestris*	Kraslava (E Latvia)	5	*Vaccinio uliginosi–Pinetum typicum*
Birkmane 1964	*Alnus glutinosa*	Kraslava (E Latvia)	1*	*Circaeo–Alnetum*

* No. 1 in Table 7.

mary, coniferous wetland forests (*Vaccinio–Piceetea*) do not have standing water above the surface, they have lower values of nitrogen and soil reaction (especially low in pine bogs). There are no principal differences among wetland forests in Ellenberg's figures (Ellenberg *et al.* 1992) for

Table 6. Ecological and phytogeographical variation of Latvian wetland forest communities. 1: *Carici elongatae–Alnetum typicum*, 2: *C.e.–A.cardaminetosum*, 3: *Sphagno squarrosi–Alnetum*, 4: *Circaeo-Alnetum*, 5: *Carici remotae-Fraxinetum*; 6: *Sphagno girgensohnii–Piceetum* var. *Crepis paludosa*, 7: *S.g.–P. myrtilletosum*, 8: *S.g.–P.m.* var. *Pinus sylvestris*, 9: *Betuletum pubescentis*, 10: *Vaccinio uliginosi-Pinetum molinietosum*, 11: *V.u.–P. typicum*, 12: *V.u.–P.t.* var. *Phragmites australis*, 13: *V.u.-P.t.* var. *Calluna vulgaris*, 14: mean % of phytogeographical subgroups in Latvian flora *sensu* Fatare (1989), Total number of plots in parentheses. * = measurements also include *Fraxinus*-dominated *Carici elongatae–Alnetum*, ** = calculation for *Sphagno girgensohnii–Piceetum* s.l.).

	1 (198)	2 (37)	3 (34)	4 (38)	5 (14)	6 (69)	7 (74)	8 (11)	9 (41)	10 (10)	11 (44)	12 (47)	13 (8)	14
DBH (mean %) classes														
I	20.0		27.1		20.2	14.0					13.7			
II	35.4		48.6		33.4	24.0					62.5			
III	18.5		22.8		18.5	29.3					19.5			
IV	24.6		0.9		24.6	29.1					4.3			
V	1.5		0.6		3.3	3.6					0			
Plots studied	16		10		11*	32**					20			
Groundwater level (cm)														
Maximum	+ 40	0	+ 5	+ 5	+ 5	+ 5	– 15	– 10	– 30	– 30	– 25	– 25	– 10	
Minimum	– 90	– 30	– 10	– 50	– 120	– 60	– 140	– 120	– 60	– 100	– 60	– 60	– 80	
Plots studied	130	20	26	29	5	20	12	4	10	4	10	10	3	
Mean height of layers (m)														
Tree	23.6	24.8	14.8	26.0	29.6	24.3	19.9	24.0	12.4	14.9	12.3	12.5	10.9	
Shrub	1.5	1.3	1.6	2.1	1.3	1.7	1.8	1.9	2.0	1.6	1.4	1.7	1.4	
Herb	0.9	0.6	0.4	0.8	0.7	1.0	0.4	0.7	0.7	0.6	1.0	1.6	0.9	
Moss	0.1	0.08	0.06	0.1	0.15	0.1	0.1	0.1	0.1	0.06	0.15	0.15	0.1	
Plots studied	51	19	18	20	14	22	16	5	19	5	14	19	6	
Peat layer (m) (extremes excluded)	0.3–1.2	0.7–1.7	1.0–2.1	0–0.6	0–0.2	0.1–1.5	0.1–1.3	0.1–0.4	0.4–0.9	0.1–0.5	0.9–4.0	0.8–3.5	0–0.5	
Plots studied	44	15	16	25	14	20	24	9	20	6	15	14	8	
Ellenberg´s indicator values (mean)														
Nitrogen	6.7	7.2	5.3	7.6	7.9	5.7	5.2	5.2	4.2	2.2	1.9	2.1	1.8	
Light	6.4	5.8	6.3	6.3	5.4	6.8	4.1	6.9	5.9	7.0	7.8	7.5	7.8	
Soil reaction	6.3	6.3	5.7	7.2	7.7	5.5	4.3	4.6	4.0	2.5	1.8	2.7	1.9	
Moisture	7.9	7.4	8.5	7.2	7.4	6.5	5.2	6.0	8.2	8.0	8.8	8.6	8.6	
Oceanic–continental distribution of species (%)														
Slightly oceanic	35.9	31.0	30.1	39.2	40.0	36.4	35.2	35.9	40.1	40.4	41.8	41.2	41.8	30.7
Suboceanic	15.0	17.1	8.3	19.8	18.5	8.8	10.0	9.4	12.1	8.9	3.4	7.2	3.2	26.2
Subcontinental	8.1	8.2	14.1	4.5	13.7	11.9	10.4	10.0	13.0	10.9	13.1	11.4	11.9	10.3
Continental	7.9	9.4	7.7	9.9	10.1	15.1	11.1	11.3	14.6	24.0	29.6	21.6	29.0	12.5
Indifferent	33.1	34.3	39.8	26.6	17.7	27.8	33.3	33.4	20.2	14.5	12.1	18.6	14.1	7.7
Other (litoral, oceanic, etc.)	0	0	0	0	0	0	0	0	0	1.3	0	0	0	12.6
Sectoral distribution of species (%)														
Euroasian (s.l.)	51.3	55.7	47.3	46.0	52.5	54.5	53.9	55.5	47.8	47.1	35.3	43.6	40.0	44.5
Circumpolar	18.4	19.9	28.6	22.0	10.7	20.0	18.6	18.5	28.9	34.0	50.7	34.3	41.6	20.7
Cosmopolitic	3.3	2.8	5.9	2.3	0	2.2	2.4	2.4	2.4	4.8	2.0	5.8	3.3	2.1
European	13.3	8.5	6.8	16.7	28.0	7.9	8.0	7.7	8.8	6.9	6.7	6.4	6.4	26.0
Euroamerican (s.l.)	13.7	13.1	11.4	13.0	8.8	15.4	17.1	15.9	12.1	7.2	5.3	9.9	8.7	6.7
Zonal distribution of species (%)														
Polyzonal	52.1	57.0	59.0	46.9	31.1	54.9	60.0	63.3	67.1	68.8	68.0	67.2	67.4	40.9
Boreal–temperate	10.7	10.9	17.4	9.6	9.7	20.5	11.9	12.1	15.6	18.8	23.8	17.7	22.5	8.2
Temperate	6.9	3.8	5.2	1.6	2.8	3.7	2.7	2.3	4.9	3.6	1.4	3.2	3.4	9.2
Temperate–submeridional	30.1	27.9	18.4	39.9	55.0	20.9	25.2	22.2	12.4	8.4	4.1	10.9	4.6	33.0
Submeridional + submerid.–merid.	0.2	0.4	0	2.0	1.4	0	0.2	0.1	0	0	0	0	0	7.0
Boreal + arctoboreal	0	0	0	0	0	0	0	0	0	0.4	2.7	1.0	2.1	1.7

light and moisture and among the mean height of the lower vegetation layers (except in *Vaccinio uliginosi–Pinetum typicum* var. *Phragmites australis* due to abundant reed in the herb layer).

The presence of a peat layer (woody–herbaceous, woody–moss–herbaceous) is an important feature in most of the communities, however, this varies considerably.

Analysis of DBH classes points to quite a low number of high diameter trees in Latvian mature wetland forest communities. This cannot be explained by selective (commercial) logging of big trees because such an activity has not been generally practiced in Latvian wetland forests. The reason for this may be that up till now clear-cutting has always been the dominant method in Latvian forestry and, thus, the recognized high-diameter (biologically old) trees are, in fact, some incidentally non-felled ones (mostly oak, lime, rarely spruce) since the last clear-cutting. As indicated in Material and methods, 80–100-year-old stands were examined here.

The phytogeographical analysis points to a considerable deviation from the mean figures found for Latvian flora (Fatare 1989). These features have already been summarized for the peatland forests (Prieditis 1993c). In all communities indifferent, polyzonal and boreal–temperate species slightly to considerably exceed the mean values for such subgroups in Latvian flora. Those of the communities restricted at the *Sphagnum*-rich bogs also phytogeographically (obvious increase of circumpolar, boreal, continental species) point to their specific habitats. Only *Carici remotae–Fraxinetum* is rich in European species, whereas this sectoral group is unimportant in the other communities. Almost no species belonging to litoral (s.l.), eu-oceanic or oceanic groups occur in the wetland forests, although such species comprise 12.6% of the Latvian flora (continentality analysis).

Summary on the Latvian wetland forests

In this paper, some supplementary data treatment based on the synoptical tables has been performed for a better visual comprehension of the described syntaxa. These, therefore, represent something like a "mean" community (defined as "relevès" in Figs. 5 and 6) of each of the 13 wetland communities distinguished in Latvia.

DCA-ordination of species (Fig. 4) and "relevès" (Fig. 5) show a distinct pattern coinciding well with the various community features briefly summarized in Table 6. Conditionally, four species groups (Fig. 4) can be recognized, and the species of *Querco–Fagetea* (*Alno-Ulmion*) and *Dicrano–Pinion* syntaxa seem to be more restricted to the alliances they represent than those of *Vaccinio–Piceion* and *Alnion*. However, it has to be kept in mind that many of the species presented there are, in fact, the character species of non-woody mires and bogs (*Oxycocco–Sphagnetea*, *Scheuchzerio–Caricetea fuscae*, etc.).

Aegopodium podagraria, Lonicera xylosteum, Carex remota, Ranunculus cassubicus, Ulmus glabra, Tilia cordata and *Acer platanoides* have high frequencies (at least III) in *Alno–Ulmion* wetlands; these species have almost never been recorded in the other alliances of wetland forests. Such species as *Athyrium filix-femina, Filipendula ulmaria, Urtica dioica, Crepis paludosa, Cirsium oleraceum* and *Geum rivale* are widespread in most of the syntaxa in Latvian wetland forests (except *Dicrano–Pinion*), and can be recorded in high frequency and cover-abundance in mesotrophic and eutrophic habitats.

Although low-frequency species were included in the GROUPAGE analysis (Fig. 6) compared with DCA (see Methods), an unexpected association of *Betuletum pubescentis* with *Sphagno squarrosi–Alnetum* (*Alnion* syntaxon) but not with *Dicrano–Pinion* syntaxa has been recognized. Thus, *Betuletum pubescentis* is placed separately in the ordination diagram of "relevès" (Fig. 5), between the mesotrophic *Alnion* and *Vaccinio–Piceion* and meso–oligotrophic *Dicrano–Pinion* syntaxa. However this, without any doubt, belongs to the rich *Dicrano–Pinion* community.

At the similarity level of 0.4 (Fig. 6), three groups can be distinguished: oligotrophic *Dicrano–Pinion*, eutrophic *Alno–Ulmion* and a slightly fused group of *Alnion* and *Vaccinio–Piceion* communities (except *Betuletum pubescentis*). However, at SR 0.5 there is an almost precise correspondence of communities to the syntaxonomical groups they represent (again, except *Betuletum pubescentis*). This figure correlates well with the ordination data (Figs. 4 and 5). The great number

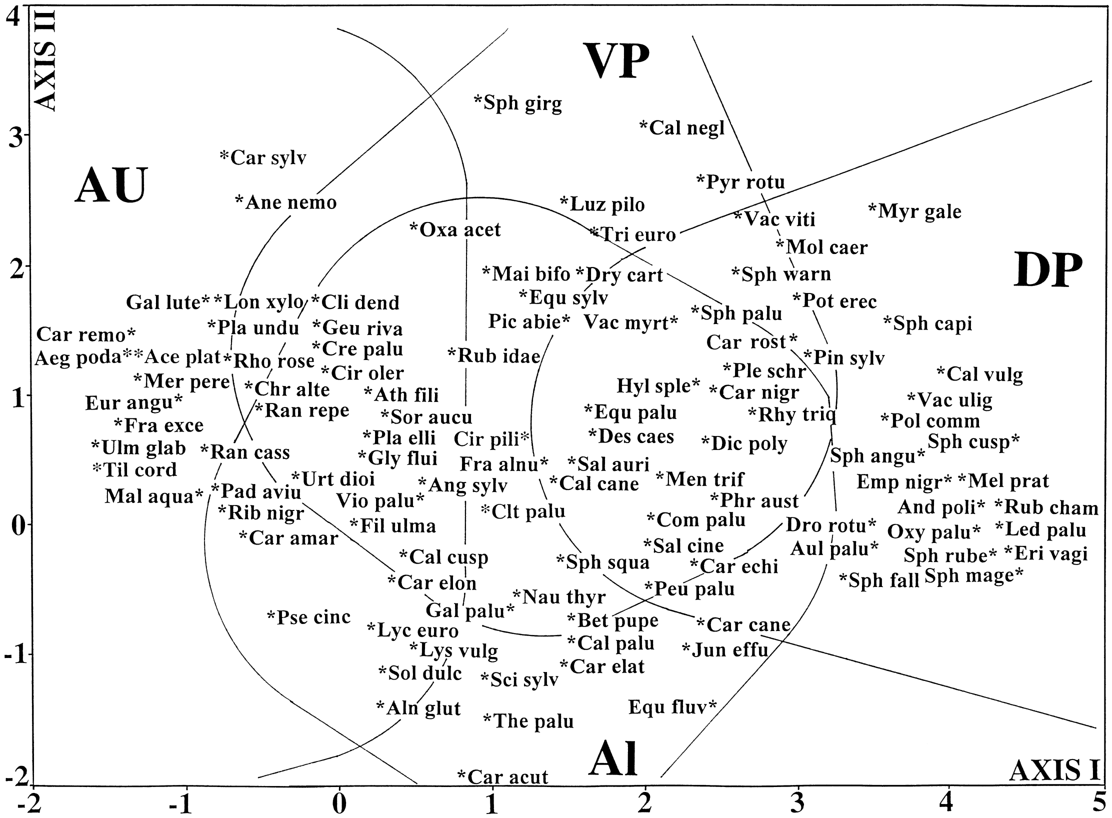

Fig. 4. DCA ordination with axes I and II of species most frequently found in Latvian wetland forests (see Appendix for the abbreviated names of species; species groups are indicated as follows: AU (*Alno–Ulmion* species), VP (*Vaccinio–Piceion* species), DP (*Dicrano–Pinion* species), Al (*Alnion* species)).

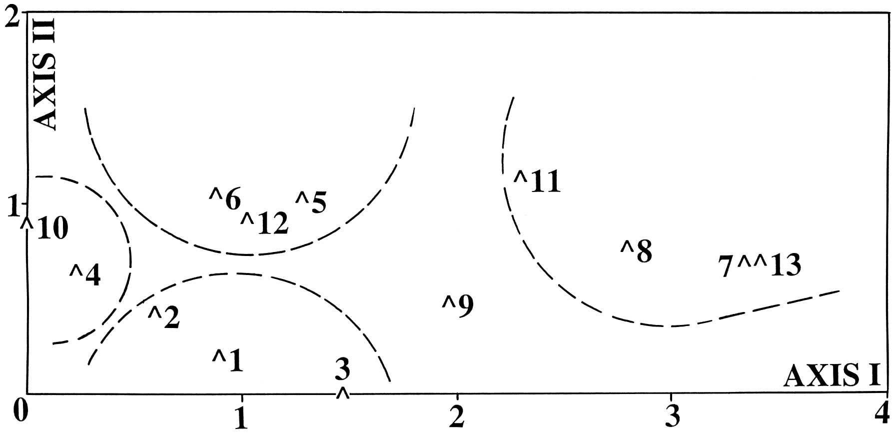

Fig. 5. DCA ordination diagram with axes I and II of Latvian wetland forest communities ("mean relevès" *sensu* synoptical table). Communities are indicated as follows: *Alnetea glutinosae* — *Carici elongatae–Alnetum typicum* (1), *C.e.–A. cardaminetosum* (2), *Sphagno squarrosi–Alnetum* (3); *Querco–Fagetea* — *Circaeo–Alnetum* (4), *Carici remotae–Fraxinetum* (10); *Vaccinio–Piceetea, Vaccinio–Piceion* — *Sphagno girgensohnii–Piceetum myrtilletosum* (5), *S.g.–P. var. Crepis paludosa* (6), *S.g.–P. myrtilletosum var. Pinus sylvestris* (12); *Vaccinio–Piceetea, Dicrano–Pinion* — *Vaccinio uliginosi–Pinetum typicum* (7), *V.u.–P.t. var. Phragmites australis* (8), *V.u.–P.t. var. Calluna vulgaris* (13), *V.u.–P. molinietosum* (11), *Betuletum pubescentis* (9).

of selective species in *Alno–Ulmion* and *Dicrano–Pinion,* as compared with *Alnion* and *Vaccinio–Piceion* (see Fig. 4), makes it possible to easily separate the first two alliances. There are numerous common species between *Vaccinio–Piceion* and *Alnion,* with very few selective species strictly confined to these alliances. *Betuletum pubescentis* (*Dicrano–Pinion* syntaxon) has no selective species at all (see also Table 3). In fact, it contains species from 3 alliances, favouring, however the elements of boreal coniferous woodland.

Concluding remarks

Phytogeographically, Latvia lies in the territory where both nemoral and boreal, Atlantic and continental vegetation intersect. This situation may account for the uncommon richness, in European terms, of wetland forest types, supported by the management history and hydrological peculiarities. Typical Central European syntaxa (e.g. *Carici remotae–Fraxinetum*), at the marginal area, specific to the NNE European spruce wetlands (*Sphagno girgensohnii–Piceetum*), and species-poor boreal pine bogs (*Vaccinio uliginosi–Pinetum*) co-occur there.

Aiming at an increased knowledge of these habitats, still semi-natural wetland areas, the study has also focused on syntaxonomical issues, particularly on *Picea abies*- and *Alnus glutinosa*-dominated wetlands.

The proposed syntaxonomical structure, well supported by the site ecology, might be the basis for extended community studies, especially with respect to their biodiversity evaluation, species co-existence and the pattern changes after disturbance.

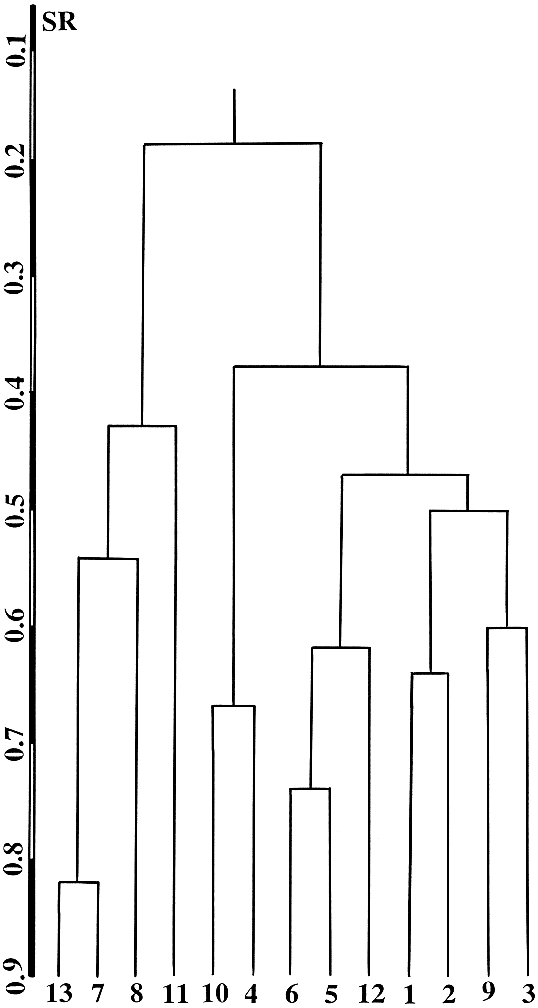

Fig. 6. The cluster dendrogram by GROUPAGE of Latvian wetland forest communities ("mean relevès" *sensu* synoptical table). SR-similarity ratio (numbers of communities — see Fig. 5 caption).

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Appendix. List of species with the abbreviations used in the figures (DCA-ordination, TWINSPAN-classification).

Ace plat	*Acer platanoides*
Aeg poda	*Aegopodium podagraria*
Aln glut	*Alnus glutinosa*
And poli	*Andromeda polifolia*
Ane nemo	*Anemone nemorosa*
Ang sylv	*Angelica sylvestris*
Ath fili	*Athyrium filix-femina*
Aul palu	*Aulacomnium palustre*
Bet pupe	*Betula pubescens* et *B. pendula*
Cal cane	*Calamagrostis canescens*
Cal cusp	*Calliergonella cuspidata*
Cal negl	*Calamagrostis neglecta*
Cal palu	*Calla palustris*
Cal vulg	*Calluna vulgaris*
Car acut	*Carex acutiformis*
Car amar	*Cardamine amara*
Car cane	*Carex canescens*
Car echi	*Carex echinata*
Car elat	*Carex elata*
Car elon	*Carex elongata*
Car nigr	*Carex nigra*
Car remo	*Carex remota*
Car rost	*Carex rostrata*
Car sylv	*Carex sylvatica*
Chr alte	*Chrysosplenium alternifolium*
Cir oler	*Cirsium oleraceum*
Cir pili	*Cirriphyllum piliferum*
Cli dend	*Climacium dendroides*
Clt palu	*Caltha palustris*
Com palu	*Comarum palustre*, syn. *Potentilla palustris*
Cre palu	*Crepis paludosa*
Des caes	*Deschampsia caespitosa*
Dic poly	*Dicranum polysetum*
Dro rotu	*Drosera rotundifolia*
Dry cart	*Dryopteris carthusiana*
Equ fluv	*Equisetum fluviatile*
Equ palu	*Equisetum palustre*
Equ sylv	*Equisetum sylvaticum*
Emp nigr	*Empetrum nigrum*
Eri vagi	*Eriophorum vaginatum*
Eur angu	*Eurhynchium angustirete*
Fil ulma	*Filipendula ulmaria*
Fra alnu	*Frangula alnus*
Fra exce	*Fraxinus excelsior*
Gal lute	*Galeobdolon luteum*
Gal palu	*Galium palustre*
Geu riva	*Geum rivale*
Gly flui	*Glyceria fluitans*
Hyl sple	*Hylocomium splendens*
Jun effu	*Juncus effusus*
Led palu	*Ledum palustre*
Lon xylo	*Lonicera xylosteum*
Luz pilo	*Luzula pilosa*
Lyc euro	*Lycopus europaeus*
Lys vulg	*Lysimachia vulgaris*
Mai bifo	*Maianthemum bifolium*
Mal aqua	*Malachium aquaticum*
Mel prat	*Melampyrum pratense*
Men trif	*Menyanthes trifoliata*
Mer pere	*Mercurialis perennis*
Mol caer	*Molinia caerulea*
Myr gale	*Myrica gale*
Nau thyr	*Naumburgia thyrsiflora*, syn. *Lysimachia thyrsiflora*
Oxa acet	*Oxalis acetosella*
Oxy palu	*Oxycoccus palustris*
Pad aviu	*Padus avium*
Peu palu	*Peucedanum palustre*
Phr aust	*Phragmites australis*
Pic abie	*Picea abies*
Pin sylv	*Pinus sylvestris*

(Continues …)

Appendix. Continued.

Pla elli	*Plagiomnium ellipticum*	Sph ang	*Sphagnum angustifolium*
Pla undu	*Plagiomnium undulatum*	Sph capi	*Sphagnum capillifolium*
Ple schr	*Pleurozium schreberi*	Sph cusp	*Sphagnum cuspidatum*
Pol comm	*Polytrichum commune*	Sph fall	*Sphagnum fallax*
Pot erec	*Potentilla erecta*	Sph girg	*Sphagnum girgensohnii*
Pse cinc	*Pseudobryum cinclidioides*	Sph mage	*Sphagnum magellanicum*
Pyr rotu	*Pyrola rotundifolia*	Sph palu	*Sphagnum palustre*
Ras cass	*Ranunculus cassubicus*	Sph rube	*Sphagnum rubellum*
Ran repe	*Ranunculus repens*	Sph squa	*Sphagnum squarrosum*
Rho rose	*Rhodobryum roseum*	Sph warn	*Sphagnum warnstorfii*
Rhy triq	*Rhytidiadelphus triquetrus*	The palu	*Thelypteris palustris*
Rib nigr	*Ribes nigrum*	Til cord	*Tilia cordata*
Rub cham	*Rubus chamaemorus*	Tri euro	*Trientalis europaea*
Rub idae	*Rubus idaeus*	Ulm glab	*Ulmus glabra*
Sal auri	*Salix aurita*	Urt dioi	*Urtica dioica*
Sal cine	*Salix cinerea*	Vac myrt	*Vaccinium myrtillus*
Sci sylv	*Scirpus sylvaticus*	Vac viti	*Vaccinium vitis-idaea*
Sol dulc	*Solanum dulcamara*	Vac ulig	*Vaccinium uliginosum*
Sor aucu	*Sorbus aucuparia*	Vio palu	*Viola palustris*