

# Vegetation ecology and flooding dynamics of boreal aro wetlands

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Aro wetlands are a poorly-known, hydrologically extreme inland habitat type outside permanent waterbodies, often occurring in weekly paludified parts of peatlands. They are characterized by alternating flood and drought periods. We studied these habitats in the mid-boreal zone in the coastal part of Northern Ostrobothnia (65°N). We made classification (Cluster analysis) and ordination analyses (NMDS) with small-sized relevés and measured the water table fluctuations from four sites over a seven-year-period in order to reveal the depth and duration patterns of flooding and the durations of dry periods in various aro communities. These were compared with Ellenberg's indicator values for moisture. Ellenberg's indicator values for soil reaction (checked from Finnish material) and nitrogen were applied for evaluating the significance of pH as an ecological gradient in aro wetlands and their fertility and productivity characteristics. A hydrological habitat template for aro wetlands could be compiled on the basis of the depth and duration characteristics of flooding and the duration characteristics of dry periods. A gradient comparable to the poor-rich gradient of mires was also detected. All the aro wetland types proved to be low-productive. The most essential ecological factor for aro wetlands was named "flood and desiccation influence". It seemed to cause a decrease in species number as a result of natural disturbance.

Key words: disturbance, Ellenberg's indicator values, fen, ordination, pH, species richness, water level fluctuations, wetland vegetation

## Introduction

Aro wetlands are a specific type of treeless, temporary wetland with vegetation composed mainly of typical fen species but with practically no peat layer. They are characterised by large water-level fluctuations, as compared with those

in boreal peatlands. Both flood types (regular or irregular) and seasonal drought are significant. A preliminary description of the habitat type was given by Laitinen *et al.* (2005b) from a set of localities in Northern Ostrobothnia, although descriptions from single localities with other names ("flooded heath") have been provided

earlier from the study area (Jalas 1953) and from southern Finland (Valpas 1964). The concept “aro” is derived from the Finnish language and means a flat depression on a sand or till substratum. In our study area, which lies in flat Northern Ostrobothnia, such flat depressions may even be larger (several hectares) when occurring in connection with mires as mire–aro wetland systems between ancient raised beach ridges (Laitinen 1990, Laitinen *et al.* 2005b). They occupy the lowest zones in these systems and act as temporary flood depressions. Sedge-like plants (*Carex lasiocarpa*, *Juncus filiformis*, *Carex nigra*, *Rhynchospora fusca*) are characteristic for these aro wetlands, herbs are totally lacking in the inland habitats and mosses are scanty. The present research concerns the habitat type occurring in connection with flat mire systems and with a sandy substratum beneath the organic layer.

Natural disturbance is an important factor shaping plant communities in wetland environments (Keddy 2000). Well-known habitats of this type are seashores and lakeshores, which experience disturbance by waves, wind, water level fluctuations, ice scouring and plant debris. Also well-known European dune slacks are characterised by large, seasonal water table fluctuations (Grootjans *et al.* 1998). The aro wetland habitat type is comparable to the dune slacks in that the substratum is permeable (sandy), water-level fluctuations are large and both flood (hydroperiod) and a drought periods occur. The principal plant communities and the main features of the ecology of the aro wetlands are well known (Laitinen *et al.* 2005b). The variety in the depth of flooding and flooding dynamics in relation to various aro plant communities (vegetation types), however, is not known. In addition, the significance of natural disturbance (Grime 1977, 1979, Grime *et al.* 1988, Keddy 2000) with regard to plant community distribution within aro wetlands has not been discussed before, and the possible relation of general mire gradients (Sjörs 1948, Eurola *et al.* 1984, Økland *et al.* 2001) with aro wetlands is unknown.

The principal aim of this investigation is to study the effects of the depth and duration of flooding and the duration of dry periods on the plant community structure (vegetation types) and the species richness of aro wetlands. A hydro-

logical habitat template for aro wetlands is presented, with a proposal for assessing the principal mechanism by which the variety in water level fluctuations affects the occurrence of various aro communities in different aro sites. The information received with Ellenberg’s indicator values for “moisture” is compared with that obtained through measurements. Secondly, the possible occurrence of the “poor–rich” mire gradient (Sjörs 1948, 1952) and the fertility and productivity characteristics of aro wetlands are evaluated on the basis of Ellenberg’s indicator values for “soil reaction” and “nitrogen” (Ellenberg *et al.* 1992). The relevancy of Ellenberg’s “soil reaction” (central Europe) for boreal conditions was checked from Finnish pH-material concerning fens.

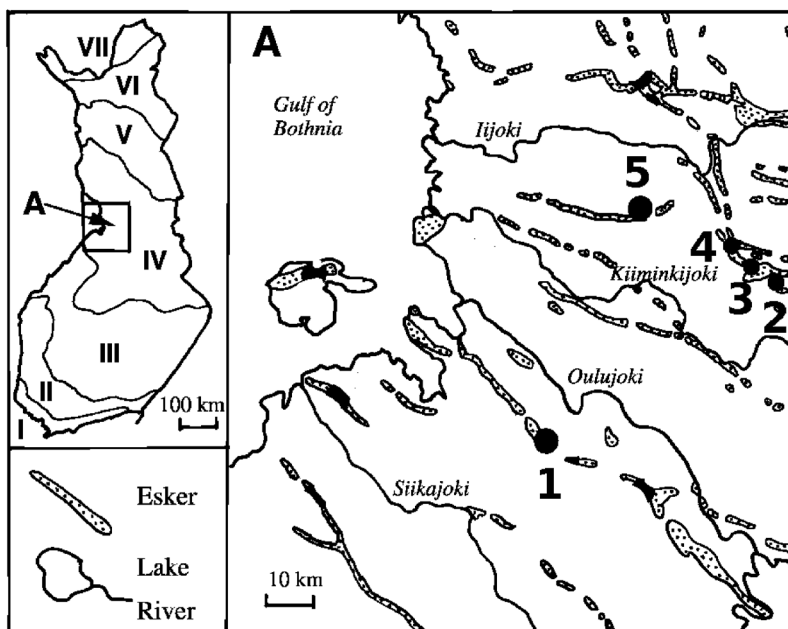
## Material and methods

### Study area, study localities and weather conditions during the monitoring period

The study area lies in a flat lowland area in Northern Ostrobothnia by the Gulf of Bothnia (Fig. 1). The area belongs to the middle boreal zone (Hämet-Ahti, 1981) and the mean annual temperature is 1–2 °C (Alalammi 1987). The localities sampled are situated in areas with siliceous bedrock, without considerable amounts of basic or carbonate minerals (Korsman *et al.* 1997). The lowland area was submerged in the Baltic Sea after the last glaciation. Sandy raised beach ridge fields are typical of parts of the area and mires have spread largely over various glacial, littoral and aeolian deposits. Aro wetlands are typically situated in flat depressions between raised beach ridges. The flat depressions are mostly filled with peat but aro wetlands occur close to eskers, from which the sets of raised beach ridges branch.

The water-table monitoring was carried out at locality 1 (Fig. 1) during snow-free periods in 1997–2005. The melting of snow at the beginning of May causes a spring flood in water-courses, wetlands and in some of the mires. The year 1998 was exceptionally wet with very large amounts of rain during the summer. In years 1999, 2000 and 2002 the autumns were drier than normal.

**Fig. 1.** Study area (A) and study localities (1–5) in Northern Ostrobothnia, Finland. The mire zones of Finland shown in the map include the plateau bog zone (I), the concentric bog zone (II), the eccentric bog zone (III), the southern aapa mire zone (IV), the main aapa mire zone (V), the northern aapa mire zone (VI) and the palsa mire zone (VII) (Ruuhijärvi & Hosiaisuus 1988). Study localities include the Resssun-aro area (1), Leväsuo area (2), Kälväsvaara area (3), Kokkomaa area (4) and Hirvisuo area (5).



### Vegetation data and subjective classification of vegetation

The vegetation data analysed in this paper included 44 relevés from five localities (Fig. 1). The relevés were subjectively classified into the *a priori* vegetation types — five relevés on the average per one type (Table 1). Groups I to V are aro wetland types described by Laitinen *et al.* (2005b), while group VI is a rarer aro type resembling type I. The other types (which were from locality 5, Fig. 1) were added to the data set as “outgroups” to reveal the relationship of the aro types to other vegetation types. These outgroups did not influence numerical classification or ordination within the aro groups. All the aro wetland types are species-poor with one or two dominant species.

The size of relevés in the aro wetland data was 0.5 m<sup>2</sup> and that of ClimMnfe, TrScomfe and pEVT 0.25 m<sup>2</sup>. The nomenclature of vascular plants follows Hämet-Ahti *et al.* (1998) and that of bryophytes Ulvinen *et al.* (2002). *Polytrichum commune* (incl. *P. schwarzii*) is treated collectively. *Sphagnum* aggr. refers to *S. annulatum* (incl. *S. jensenii*, Isoviita 1966) and *S. majus*. The thickness of the organic layer was measured by means of a metallic rod for each relevé. The values given by the method tend to be slightly

too high, because the rod tends to penetrate into the sand below the organic layer.

### Numerical vegetation analysis

Vegetation was analysed using non-metric multidimensional scaling (NMDS) and the hierarchic cluster analysis. Both the analyses were based on the Bray-Curtis dissimilarity measure (Faith *et al.* 1987). The data were cover-percentage values, but the influence of high cover values was reduced using square root transformation. In addition, we used Wisconsin double standardization, or divided each species by its maximum, and standardized each site to equal total. In general, this standardization facilitates the finding of main gradients (Faith *et al.* 1987), and together these methods provide the most robust, effective means of unconstrained ordination (Minchin 1987). The data were heterogeneous, and 46.8% of all dissimilarities were between relevés sharing no species. Therefore we used step-across dissimilarities, or replaced non-shared dissimilarities with shortest paths across the sites sharing some species with the compared sites (Williamson 1978, De'ath 1999). The ordination diagrams were interpreted by fitting smooth thinplate spline surfaces. The degree of smooth-

ing was determined with crossvalidation (Wood 2003). The data were clustered using an average linking method on the same dissimilarity matrix as used in the ordination (Anderberg 1973). All statistical analyses were performed in the R statistical environment (R Development Core Team 2006) using package *vegan* (Oksanen *et al.* 2006) in the ordination analysis.

## Water table fluctuations

Water table fluctuations during max. eight years (late summer 1997–2005) were measured at four sites (Mudflat, Rhyfuaro, Carnigaro, with heath forest as a reference site outside the vegetation material). The monitoring was performed during snow-free seasons with several visits per season

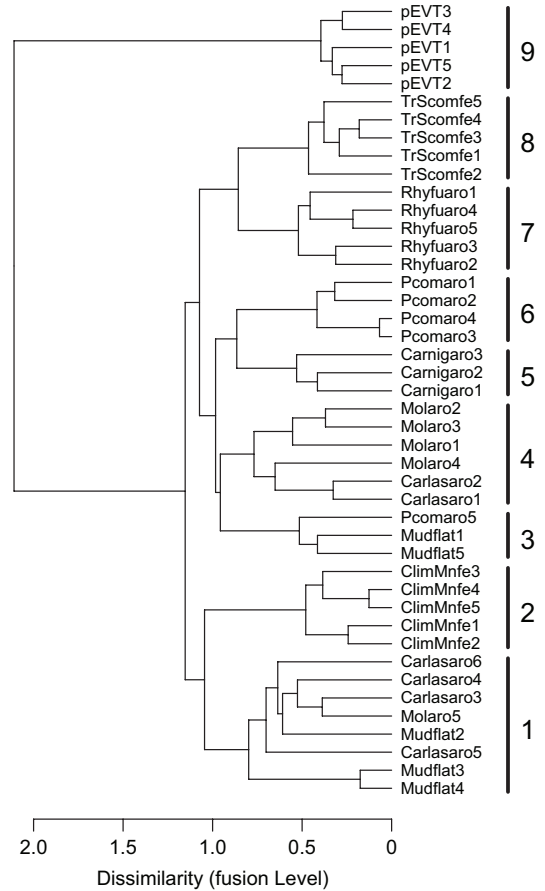
**Table 1.** *A priori* vegetation types used in this article: types I–V are aro wetland types described by Laitinen *et al.* (2005b), type VI is a rarer aro type resembling type I and types VII–IX are “outgroups”, which are added to the data to elucidate the relationship of the aro vegetation to other vegetation. Species in parentheses refer to species with very small coverages and to species with coverages ranging from high to low values.

Abbreviation	Vegetation type	Species	Occurrence
I. Polcomaro	<i>Polytrichum commune</i> aro wetland	Dominants: <i>Polytrichum commune</i> Others: <i>Carex nigra</i> , <i>Juncus filliformis</i> , ( <i>Carex lasiocarpa</i> )	Common aro wetland type, at the end of wetland chains against esker formations
II. Molaro	<i>Molinia caerulea</i> aro wetland	Dominants: <i>Molinia caerulea</i> Others: <i>Sphagnum compactum</i> , <i>Polytrichum commune</i> , <i>Gymnocolea inflata</i>	Rare type, in marginal parts of aro wetlands
III. Rhyfuaro	<i>Rhynchospora fusca</i> aro wetland	Dominants: <i>Rhynchospora fusca</i> , ( <i>Sphagnum compactum</i> ) Others: <i>Eriophorum angustifolium</i>	Quite rare type, in marginal parts of aro wetlands (sometimes between Molaro and Carlasaro)
IV. Carlasaro	<i>Carex lasiocarpa</i> aro wetland	Dominants: <i>Carex lasiocarpa</i> , ( <i>Sphagnum platyphyllum</i> , <i>Sphagnum annulatum</i> , <i>Sphagnum majus</i> ) Others: <i>Eriophorum angustifolium</i> , <i>Juncus filliformis</i>	Common type, in the relatively low-lying central parts of most aro wetlands; a transition to <i>Carex lasiocarpa</i> and <i>Eriophorum angustifolium</i> fens common
V. Mud flat	Mud flat	Sparsely growing <i>Juncus supinus</i> , <i>Carex lasiocarpa</i>	Rare type, in the lowest-lying sites in aro wetlands
VI. Carnigaro	<i>Carex nigra</i> aro wetland	Dominants: <i>Salix repens</i> , <i>Carex nigra</i> Others: <i>Polytrichum schwarzii</i> , ( <i>Calamagrostis epigejos</i> , <i>Carex elata</i> subsp. <i>omskiana</i> )	Rare, resembles young aro wetlands on the coast
VII. ClimMnfe	<i>Carex limosa</i> – <i>Menyanthes trifoliata</i> fen (mud bottom flark fen, Eurola <i>et al.</i> 1984, 1995)	Dominants: <i>Carex limosa</i> , <i>Menyanthes trifoliata</i>	Common mire site type in aapa mire centres
VIII. TrScomfe	<i>Trichophorum cespitosum</i> – <i>Sphagnum compactum</i> fen (Ruuhijärvi 1960, Fransson 1972)	Dominants: <i>Trichophorum cespitosum</i> , <i>Sphagnum compactum</i>	Common mire site type in thin-peated, sandy substratum within aapa mires, also in slope mires, often as a contact community to aro wetland
IX. pEVT	Paludified <i>Empetrum</i> – <i>Vaccinium</i> heath forest (Kalela 1961, Kalliola 1973)	Dominants: <i>Vaccinium vitis-idaea</i> , <i>V. uliginosum</i> , <i>Empetrum nigrum</i> , <i>Pleurozium schreberi</i> Others: <i>Sphagnum capillifolium</i> , <i>Hylocomium splendens</i>	Paludified type of common “dryish heath forest site type”, occurs on sandy mire margins

(the later part of the period was monitored with sparse intervals only). A combination of shallow groundwater wells and deep groundwater tubes installed into the mineral soil was used. At the measuring point for Carnigaro, the groundwater tube (up to 1 m deep) did not reach the groundwater table level, which was measured from a deeper groundwater tube provided by the Environment Centre of Northern Ostrobothnia about 20 m away from the Carnigaro measuring point. The height difference in the groundwater table level between the Carnigaro measuring point and the deep groundwater tube must be small because the gradient of the groundwater table in permeable sand is small.

### Other ecological characteristics

For each relevé, we calculated the average Ellenberg's indicator values for "moisture", for "soil reaction" and for "nitrogen" (Ellenberg *et al.* 1992). Some species were missing from Ellenberg's data. The validity of Ellenberg's soil reaction values for north-central Finland was confirmed by comparing Ellenberg's result with the result obtained for eastern Finnish fen material (Tahvanainen *et al.* 2002, Tahvanainen 2004). pH values were used in this connection. Species ecological optima along the water pH gradient were estimated from the data by means of abundance weighted averaging. The estimated pH and Ellenberg's values were then fitted into the ordinations. Water pH has proved to be the most reliable indicator of the poor–rich gradient (Sjörs 1952, Tahvanainen 2004) in mires. In aro wetlands, surface water fluctuation makes it difficult to assess water pH conditions without detailed seasonal monitoring. Furthermore, the pH of surface water probably does not have similar dynamics and effects in aro wetlands as in mires. However, most of the aro-wetlands species are typically mire plants and therefore the calibration with pH, a chemical indicator of the poor–rich gradient in mires, is valid for exploring the poor–rich gradient in aro wetlands.



**Fig. 2.** Clusters (1–9) shown by the cluster analysis. See chapter 'Clustering of vegetation' and the *a priori* classification of aro wetlands.

## Results

### Clustering of vegetation and the *a priori* classification of aro wetlands

Aro wetlands and other vegetation types were separated in the classification by means of the cluster analysis (Fig. 2 and Table 1). A division with nine clusters was chosen. The clusters were arranged in the order of NMDS 1 in the ordination (Fig. 3). pEVT relevés (cluster 9) formed a cluster completely separate from aro wetlands and fens. Fens did not form a uniform group in relation to aro wetland: all the ClimMnfe relevés (cluster 2) formed a cluster that was combined with a large group dominated by the Carlasaro

relevés (cluster 1) and all the TrScomfe relevés (cluster 8) formed a group that was combined with the Rhyfuaro relevés (cluster 7). The bulk of the Polcomaro relevés (cluster 6) and all the Carnigaro relevés (cluster 5) formed two nearby clusters as did the group dominated by the Molaro relevés (cluster 4) and a small group (cluster 3) with pine seedlings in every relevé. The configuration of the aro wetland classification by means of the cluster analysis did not dramatically differ from the *a priori* classification. Mud flat, however, did not keep its position as a uniform vegetation entity in the cluster analysis, as the relevés were dispersed in several clusters at a high level of hierarchy. Three mud flat relevés were combined into the large group dominated by the Carlasaro relevés (cluster 1) and two of them were contained in a small group (cluster 3) characterised by the occurrence of pine seedlings.

### Ordination of the vegetation

In the ordination (Fig. 3), the clusters 1 and 3 including the mudflat relevés and *Juncus supinus*, were situated in extreme left in the ordination. *Juncus supinus* is an aquatic plant occurring e.g. on exposed shores with sandy bottoms (Toivonen & Lappalainen 1980). pEVT relevés (cluster 9) and pine mire species (*Vaccinium uliginosum*, *Ledum palustre* etc.; Eurola et al. 1984) and heath forest species (*Vaccinium vitis-idaea*, *V. myrtillus*, *Empetrum nigrum*; Kalela 1961) occurred in extreme right in the ordination. Thus the NMDS 1 referred to a direction of variation from aquatic (eulittoral) to dry (no-flooded) conditions and from various aro wetlands to a lawn fen and to a paludified heath forest.

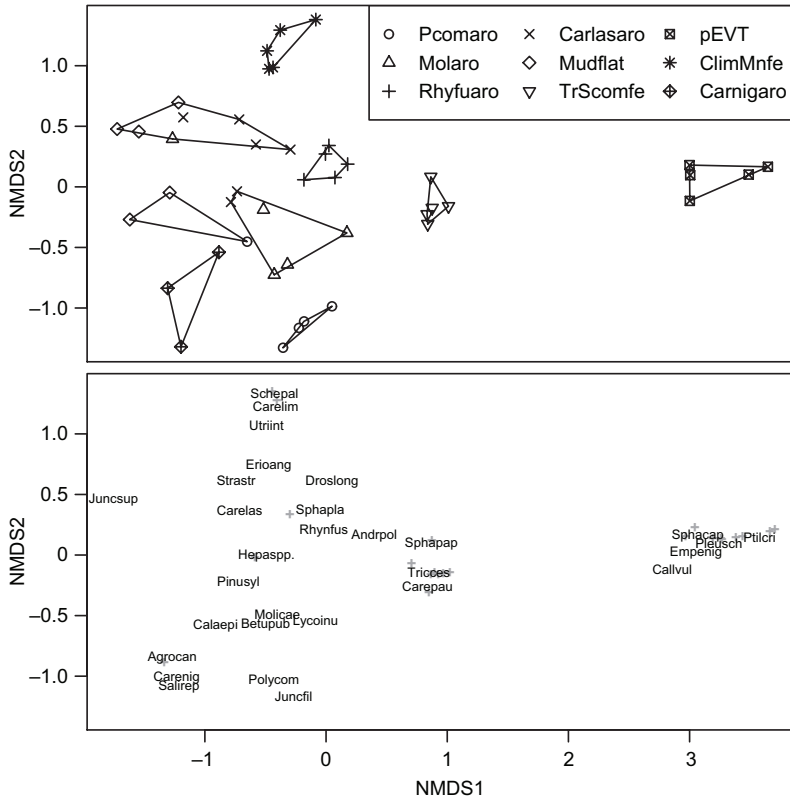
Cluster 2 (ClimMnfe) and several typical flark-fen species of a mire expanse character (*Carex limosa*, *C. chordorrhiza*, *Scheuchzeria palustris*, *Menyanthes trifoliata*, *Utricularia intermedia*) were located upmost in the ordination (Fig. 3), while the bottom part of the graph was occupied by clusters 5 (Carnigaro) and 6 (the bulk of the Polcomaro relevés). Part of the flooded heath vegetation described by Jalas (1953) from the esker–dune complex in Rokua, Northern Ostrobothnia, is nearly identical to the

vegetation of cluster 6 (see also Valpas 1964): Polcomaro and Carnigaro may be called flooded heath aro wetlands, while Molaro, Carlasaro and Rhyfuaro may be called fen aro wetlands on the basis of their species composition (dominance of fen species, e.g. *Carex lasiocarpa*, *Molinia caerulea*, partly *Rhynchospora fusca*; Eurola et al. 1984) and their location in relation to clusters 2 (flark fen) and 8 (lawn fen).

In clusters 5 and 6, some species (*Agrostis canina*, *Carex nigra*, *Juncus filiformis*) belong to a mire margin species group called disturbance indicators (Störzeiger) by Dierssen (1982). These species occur in drained mires and mires split by roads (Dierssen 1982). In the bottom half of the ordination graph, there were further species typical of some southern Finnish lakeshores (*Carex elata* subsp. *omskiana*; Mäkirinta 1977), species found in flooded meadows beside rivers in central Lapland (*Juncus filiformis*, *Molinia caerulea*, Eurola 1967), species of seasonally flooded rock depressions (*Carex nigra*, *Juncus filiformis*, *Polytrichum commune*; see Häyrén 1914, Häggström & Skytén 1987) and species of deflation basins on sandy seashores (*Polytrichum commune*, *Salix repens*; Pennanen et al. 2001). *Calamagrostis epigejos*, a typical post-fire species occurring in forests (Hämet-Ahti et al. 1998) and species of various man-made habitats (*Carex nigra*, *Juncus filiformis* and rare pioneer *Lycopodiella inundata*; see Jacquemart et al. 2002) also occurred in the bottom half. Thus in terms of species composition, the NMDS 2 dimension referred to a gradient from wet mire expanse vegetation of the aapa mire centres to an assemblage of various (mire margin and mineral soil) vegetation characterised by several kinds of man-made or natural disturbances, including disturbances arising from water-level fluctuations (Urban 2005), but also by wind and fire.

### Total cover and species richness of the vegetation

The total cover of plants per relevé formed a gradient from closed to unclosed vegetation along the NMDS 1 dimension (Fig. 4). This suggests an increase in the size of vegetation gaps from paludified heath forests to lawn fens, to



**Fig. 3.** Ordination of the vegetation. The upper panel shows the ordination of sites (relevés) and the lower panel the ordination of species. In the upper panel various plotsymbols refer to *a priori* vegetation types (Table 1) and the polygons refer to the clusters (cf. Fig. 2). In the lower panel the species are shown by their abbreviated names, but some rarer species overwritten by the more common ones are only shown as crosses. These species include Menytri, Carecho (near Carelim in the graph); Warnflu (near Hepaspp.); Careela (near Agrocan); Sphacom, Drosrot, Vaccmic, Sphabalt, Sphaten, Spharub, Eriovag (near Triccesp); Vaccoxy (near Carepau); Betunan (near Sphacap); Polyjun, Careglo, Vaccvit, Ledupal, Vacculi, Vaccmyr, Dicrpol, Hylospl (near Pleusch).

aro wetlands and flark fens, and finally to mud flats. Species richness (Fig. 4) diminished from the average of ten species in paludified heath forests to lawn fens (average 8) and to flark fens and aro wetlands. Thus it was also in line with the NMDS 1 dimension and was the lowest of all within the mudflats of aro wetlands. The species richness of aro wetlands as a whole was very low (from 1 to about 7 species per relevé).

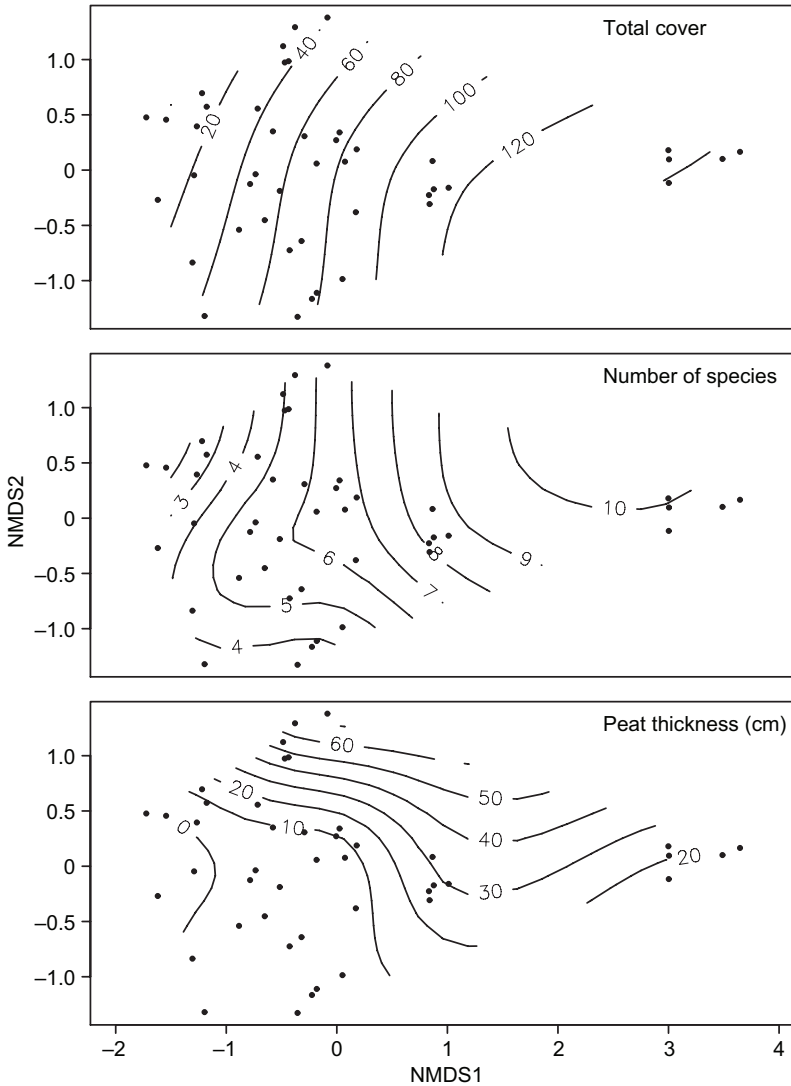
### Peat thickness

Peat was thinnest within aro wetlands and increased especially towards flark fens (cluster 2), slightly also towards lawn fens (cluster 8) (Fig. 4). Accordingly, peat thickness clearly

separated aro wetlands from fens, and there was a gradient approximately in the direction of NMDS 2 in the ordination.

### Water table fluctuations, flooding dynamics and depth of flooding

Water table fluctuations in the measured localities showed two kinds of patterns (Fig. 5): a seasonal fluctuation pattern with an annual spring flood (Carnigaro) and a longer term fluctuation (Mudflat, Rhyfuaro, Heath forest). Within the longer term fluctuation, the hydroperiod and dry season could last longer than one snow-free period. In a rainy summer, the hydroperiod of Carnigaro also lasted almost for the whole summer. In most



**Fig. 4.** Total cover, number of species and peat thickness surfaces fitted to the ordination (cf. Fig. 3).

of the aro wetlands (especially in the Carlasaro) both the seasonal and longer term fluctuation are superimposed and function together.

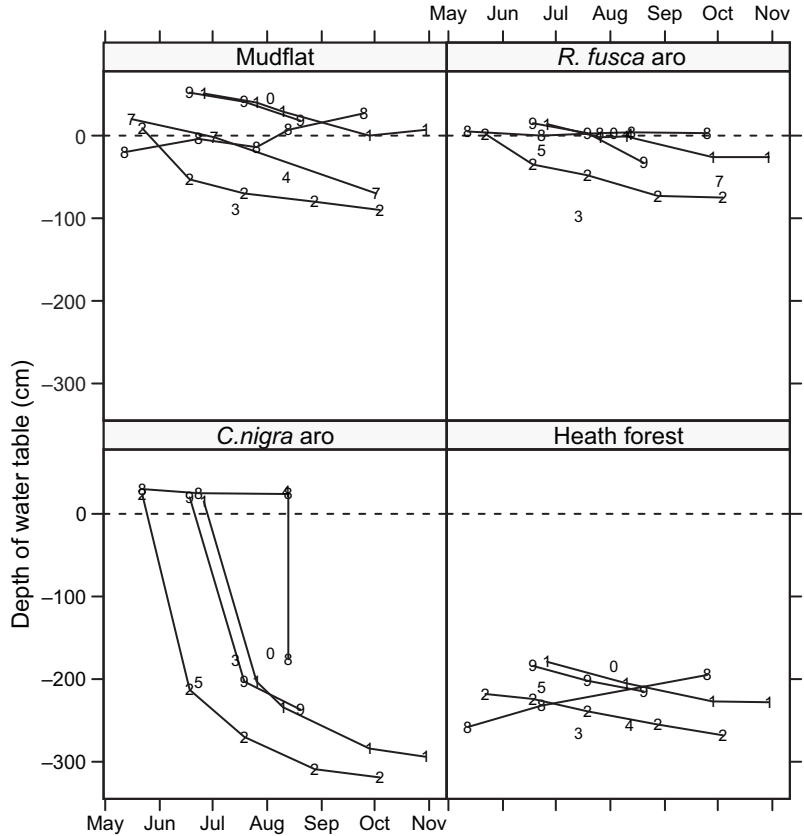
The depth of flooding was greatest in the Mudflat (maximum water level over +50 cm) and Carnigraro (Fig. 5), but lower in the Rhyfuaro. In the field, the Mudflats occupy the lowest-lying sites with the greatest depth of flooding, while the Rhyfuaro sites occupy the more elevated marginal sites with a lower depth of flooding; the Carlasaro sites are situated in an intermediate position with regard to the Mudflat and Rhyfuaro sites and accordingly the depth of flooding seems to be between that of the Mudflat and Rhyfuaro sites. At the Molaro sites, the depth of flooding

is obviously even smaller than at the Rhyfuaro, judged by the intermittent situation of the vegetation of those aro types: the Molaro sites are at higher levels when both types of vegetation occur in the same wetland chain.

#### Ellenberg's indicator values for moisture

The Ellenberg's indicator value for moisture almost followed the NMDS 1 dimension (Fig. 6). The moisture values increased in the order from pEVT to Polcomaro, to TrScomfe and Molaro (about equal values), to Carnigraro, to Rhyfuaro, to Carlasaro and to ClimMnfe and





**Fig. 5.** Snow-free-period fluctuations of the water table level presented separately for different years in a mud flat, in Rhyfuaro, in Carnigaro and in a heath forest as a reference site. The numbers in the graph mean records for the corresponding year as follows: 7 = 1997, 8 = 1998, 9 = 1999, 0 = 2000, 1 = 2001, 2 = 2002, 3 = 2003, 4 = 2004, 5 = 2005.

Mudflat (about equal values). In this case the Ellenberg's indicator value for moisture may be easily interpreted as a physiognomic gradient of the vegetation or general landscape wetness, which is comparable to a gradient from a hummock level to lawn, to carpet, and to mud bottom in mires (Sjörs 1948, Moen 1985, etc.). It also essentially coincides with the gradient of the depth of flooding in various aro wetlands: the Mudflat has larger values than the Carlasaro, followed then by the Rhyfuaro and then by the Molaro.

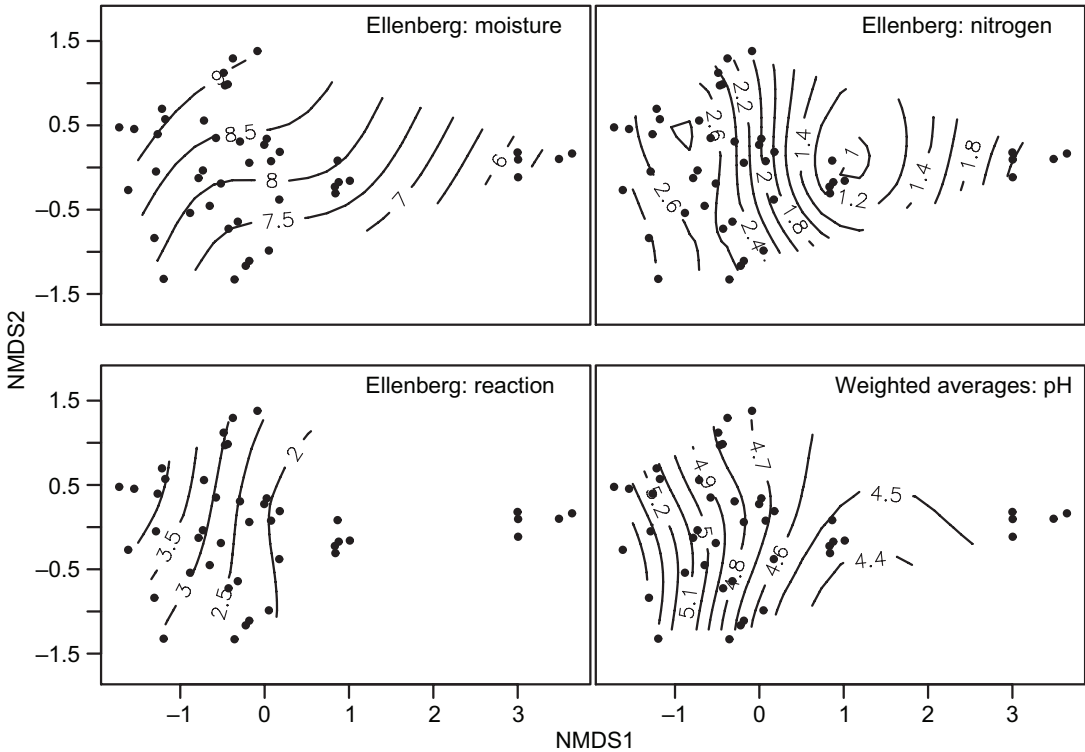
#### Ellenberg's indicator values for soil reaction and pH value in eastern Finnish fen material

Ellenberg's indicator value for reaction and the pH estimate calibrated with eastern Finnish fen data correlated with the NMDS 1 dimension i.e. the general landscape wetness (Fig. 6): the

least acidic reaction and highest pH values were suggested for mud flats, which are at times very watery. The pH calibrated with eastern Finnish fen data suggested a range of pH from 4.6 to 5.4 for aro wetlands, the lowest values for the TrScomfe (below 4.5) and values 5.5–4.6 for the pEVT. The value for the TrScomfe represents a value typical of extremely poor fens and the pH range of aro wetlands falls in the pH ranges for moderately poor to intermediate fens and moderately rich fens (Tahvanainen *et al.* 2002, Tahvanainen 2004).

#### Ellenberg's indicator values for available nitrogen

All the studied sites were judged extremely to moderately poor with regard to available nitrogen on the basis of Ellenberg's indicator values (Fig. 6). Thus aro wetlands may be regarded as low-productive wetlands. The nitrogen value



**Fig. 6.** Ellenberg indicator values for moisture, reaction and nitrogen and pH value (weighted average) calculated for relevés by species from northeastern Finnish fen material.

was the lowest in the TrScomfe and the highest within the Carlasaro. Ellenberg's indicator value for available nitrogen showed a pattern similar to the pH calibration of eastern Finnish fen data, the lawn fen (TrScomfe) being the poorest site.

## Discussion

### Vegetational and hydrological classification of aro wetlands

The concept "wetland" has been used very little or not at all as a classification concept in different schools in northern Europe because of its extreme broadness (e.g. Eurola 1999, Moen 1999, Rydin *et al.* 1999). However, the concept, or better to say approach (Keddy 2000), leads to useful large-scale comparisons and binds together very different major habitat types (mires, aquatic ecosystems, reed marshes, etc.). In connection with aro wetlands, the approach further seems appropriate because of the transi-

tional character of the aro wetlands. Gopal *et al.* (1990) divide wetlands into three major groups: mires or peatlands, temporary wetlands, and (permanent) water bodies. Aro wetlands fall in the category of temporary wetlands in this broad classification, although they are not far from thin-peated mires either. Relatively small indicator values for available nitrogen refer to infertility and thus they may be characterised as low-productive temporary wetlands. Several major wetland types, swamps and marshes of Keddy (2000) are typically fertile and highly productive. The vascular plant vegetation of aro wetlands in general also much more resembles poor fens (e.g. tall sedge fens or flark fens, Ruuhijärvi 1960) than reed marshes situated by the Gulf of Bothnia (*Phragmites communis* meadows at the heads of bays; Siira 1970). Only low-grown *Rhynchospora fusca*, and *Molinia caerulea* form denser vascular plant stands in aro wetlands. Both of them, however, usually occur as stands of limited extent in certain aro wetlands only, typically in marginal zones.

Aro wetlands as a whole form a group comparable to high-level groups (main mire vegetation units) in the Finnish mire classification by Eurola *et al.* (1984, 1995). The major ecological difference between aro wetlands and the main mire vegetation units is the highly fluctuating water table; aro wetlands form the extreme end of the water table fluctuation gradient for mires (Laitinen *et al.* 2007). The main mire vegetation units of Eurola *et al.* (1984, 1995) include (1) hummock-level pine mires, (2) treeless poor fens, (3) treeless rich fens, (4) spring vegetation, (5) swamp vegetation, (6) spruce mires, and combination site types (e.g. treed fens). Fen aro wetlands situated in inland areas in Northern Ostrobothnia form a counterpart to treeless poor fens. Geologically young aro wetlands of the land uplift coast of the Gulf of Bothnia (Laitinen *et al.* 2005b), in turn, form a counterpart to swamp vegetation as they contain several typical swamp herbs (Tuomikoski 1955, Ruuhijärvi 1960, Eurola *et al.* 1984, 1995). These include *Lysimachia thyrsiflora* and *Potentilla palustris*; the shoreline species *Ranunculus reptans* also occurs. These species do not occur in inland aro wetlands. The fourth aro wetland main group besides the fen aro wetland, flooded heath aro wetland and mud flat pond could be called swamp-aro wetland (*Sumpf*-aro wetland).

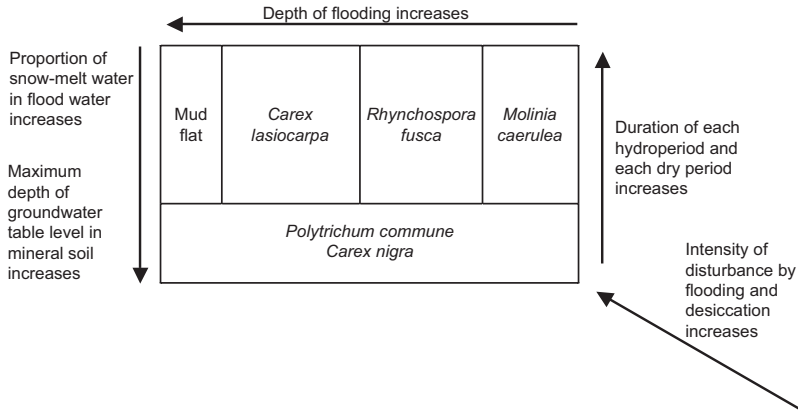
Narrower vegetation types within aro wetlands (Carlasaro, etc.) seem to be equivalent to Finnish mire site types (Cajander 1913, Ruuhijärvi 1960, Eurola *et al.* 1984, 1995) or forest site types (Kalela 1961). In nature conservation usage, the aro wetland types described as the *a priori* types in this paper proved to be valid, because in the clustering of very species-poor vegetation, random effects get more weight and artificial units may be formed (cluster 3) while ecologically useful units may disappear (mud flat). The volume of the material included in clustering in this investigation is geographically too limited to draw final conclusions of the vegetational position and variation of rare mud flats. Furthermore, Carnigaro is a local community in inland aro wetland vegetation in sandy areas in Northern Ostrobothnia. It resembles the geologically young aro wetlands of the coast of the Gulf of Bothnia, e.g. the abundant occurrence of *Agrostis canina*. A forest fire, which recently occurred in the area

(over 20 years ago), may have affected its vegetation, e.g. the occurrence of *Calamagrostis epigejos* (see also Valpas 1964).

In aro wetlands, fluctuation occurs in flooding and drying, dominated by two patterns, i.e. a seasonal fluctuation pattern with a spring flood (in some years prolonged) and a longer term fluctuation pattern with hypopediods and dry-periods even longer than one snow-free period (Fig. 5). The seasonal pattern is mainly a response to yearly snow-melt, and aro wetlands dominated by this pattern (Carnigaro, Pcomaro) might be called surface water aro wetlands. The direct effect of heavy rains in a rainy summer also considerably contributes to their hydroperiods. The longer term pattern mainly reflects the areal, long-term fluctuation in the groundwater table of mineral soils, because aro wetlands dominated by this pattern (Mudflat, Rhyfuaro) have a fluctuation pattern equal to that of a dry heath forest (large sand area). The areal long term fluctuation in groundwater table in some groundwater stations in Finland takes place in periods of several (4 to 7 and more) years (Soveri *et al.* 2001). The aro wetlands dominated by this fluctuation pattern can be called groundwater aro wetlands. Here, the concept groundwater wetland does not refer to the upwelling of groundwater from the mineral soil, and surface water wetland does not refer to limnogenic (lake or river) water. Thus the concepts are neither equal to those of Goslee *et al.* (1997), who set forth a classification of wetlands based on the water source (groundwater wetlands, seasonal and permanent surface water wetlands), nor to those of Brinson (1993), who set forth a classification based on water source (precipitation, groundwater, surface water) and corresponding wetland function (donor wetlands, receptor wetlands, conveyor wetlands). The present classification scheme for groundwater and surface water aro wetlands takes into consideration drought and hydroperiods, which are shorter in surface water aro wetlands and longer in groundwater aro wetlands.

### **Aspects of natural and man-made disturbances in aro wetlands**

A habitat template for aro wetlands, considering



**Fig. 7.** Hydrological habitat template for inland aro wetlands in Northern Ostrobothnia.

the water-level fluctuations, the natural disturbance regime caused by water-level fluctuations and the principal water origin, may be compiled on the basis of hydrologic monitoring and the aro wetland types, which are formed on the basis of dominant species (Fig. 7). Generally, the water table level fluctuations in various habitats occur over a variety of time scales and in response to regular cyclic factors (diurnal, seasonal) and particular hydrologic events (Keddy 2000). In temporary wetlands, as in aro wetlands, the water levels range from above-ground positions (flood, hydroperiod) to below-ground positions. Within the habitat template for aro wetlands, the intensity of natural disturbance is expressed as the outcome of the depth of flooding and duration characteristics of the hydroperiods and dry periods. Accordingly, aro wetlands are viewed in this template as a disturbance-driven habitat type in which the disturbance is caused by water-level fluctuations. We use the definition of disturbance by Keddy (2000): disturbance is a short-lived event that causes a measurable change in the properties of an ecological community. Short-lived refers to an event that occurs as a pulse with duration much shorter than the life span of the dominant species in the community. Biomass, diversity and species composition are listed as examples of changing properties. The wide disturbance concept by Keddy (2000) may be useful in wetlands as it is evidently powerful for both the natural disturbances (e.g. loss of biomass) and for man-made disturbances (e.g. permanent floristic changes caused by ditching).

The flood tolerance of plant species seems to separate aro wetlands from ordinary mire habitats:

*Trichophorum cespitosum* and *Molinia caerulea*, which are preferably lawn species in mires and tolerate seasonal drought well (Laitinen 1990), are not very tolerant to flood (Fig. 7). This can be seen from the fact that *T. cespitosum* occurs abundantly in the mire–aro wetland systems of the study area just beyond the flood depressions (aro wetlands), as a contact community between aro wetlands and mire habitats with a thicker peat layer and less fluctuating water table. This border of aro wetland communities and the *Trichophorum cespitosum*–*Sphagnum compactum* community is well visible in the field and in aerial photos, and it makes up a natural border of aro wetlands towards seasonally dry mires. Accordingly, *T. cespitosum* is a good indicator species separating aro wetlands from mires in our study area. The species has been encountered only exceptionally within *Molinia caerulea* aro wetlands. *Molinia caerulea* has only marginal dominance in aro wetlands in the study area (Fig. 7); the poor tolerance of *M. caerulea* to irregular floods has been stated by Kotilainen (1958). Aro wetlands do not have any natural border toward mud bottom flark fens, however. This is especially true for the Rhyfuaro, whose division from mud bottom flark fens dominated by *Rhynchospora fusca* is a matter of taste.

The intensity of disturbance is reflected in the formation of vegetation gaps. The total cover of plants formed the most regular gradient for the studied communities. Mud flat was the most extreme site with extremely small plant coverage and with a very small number of species (Fig. 7). This is in line with the observation of Urban (2005) from a sod cut stand in a degener-

ated wet heathland: in the most frequently and longest inundated relevés, the number of species per m<sup>2</sup> was very small, due to the intensity of disturbance cutting back most of the species. Within the mud flats of aro wetlands, the length of the dry period followed by the flood makes it difficult for aquatic plants to properly colonise the site. *Juncus supinus* is the only exception in the studied localities. It is a rapidly spreading, erosion resistant small helophyte (Hellsten 2001) typical of certain types of sandy lakeshores of relatively small lakes (Toivonen & Lappalainen 1980, Pakkala 1986) and may be more typical of large, regulated than large, unregulated lakes (Hellsten 2001). It is exceptionally abundant in some regulated rivers (southern Norway), with altered flow regime (Rørslett 1988). In groundwater aro wetlands we have found patchy or slightly band-like vegetation gaps especially between *Rhynchospora fusca* stands (Rhyfuaro) and *Carex lasiocarpa* or *Eriophorum angustifolium* stands (Carlasaro, transitions of aro wetlands to mud bottom flark fens). Sandy bands occur in places where there is a crease between a totally flat bottom part (Carlasaro, etc.) and the slightly sloping marginal part (Rhyfuaro) of the aro wetland — one may get an impression of a weak, exposed sandy shoreline on a dry land during a dry period (Laitinen *et al.* 2005b). The weak effect of water erosion or ice erosion seems obvious. We have also made some observations of the movement of the exact localities of *Rhynchospora* stands in aro wetlands between different years and of the disappearance of a narrow *R. fusca* zone at the aro wetland margin. According to Keddy (2000), lags of recovery mean that periodic disturbances can generate a mosaic and the rates of recovery from natural disturbances will depend upon the vegetation that persists through the disturbance, upon the influx of new propagules from adjoining areas and upon the productivity of the site. In restored, central European wet heaths *R. fusca* germinates abundantly in newly formed gaps (Kesel & Urban 1999) and spreads very easily through rhizome reproduction (Sansen & Koedam 1996, Kesel & Urban 1999). According to Wilson (1991), the species is able to respond very quickly to changing habitat conditions and according to Kesel and Urban (1999), the species requires there early-succes-

sional conditions. In established communities, it occurs in central Europe at very oligotrophic sites only, with disturbance caused by a fluctuating water table (Kesel & Urban 1999). At the boreal aro wetland sites studied here, the intensity of disturbance experienced by *R. fusca* stands is so startling that one cannot be absolutely sure about the pristine hydrologic state of those sites. The length of our hydrologic monitoring period was only seven years (which corresponds to the mean longer-term period of groundwater table fluctuation observed in some Finnish groundwater stations; Soveri *et al.* 2001) and did not involve any vegetation monitoring. Repeated vegetation inventories for long periods with permanent relevés and with mapping areas covered by *R. fusca* stands would be needed in order to assess the natural state of the sites and the population dynamics and disturbance ecology of the species in comparison with the population dynamics and disturbance ecology of the species in central Europe. The intensity of disturbance caused by the annual spring flood in surface water aro wetlands (Polcomaro, Carnigaro) is not as destructive: larger bare patches are not found. Accordingly, the vegetation gradient from bare mud flats to closed paludified heath forests, indicated by the total cover of plants and Ellenberg's moisture value, can be taken to reflect a response to disturbance resulting from repeated submergence. In mud flats, the intensity of this disturbance is highest and is lacking in paludified heath forests.

Ruderal species are typical of disturbed sites (Grime 1977, 1979), whereas in aro wetlands disturbance does not affect the temporal occurrence of ruderals, as was predicted by the Grime's theory. Limestone-poor aro wetlands occurring in inland areas in Northern Ostrobothnia are totally devoid of herbs, annual and others. Instead of ruderal species, stress strategists (Grime *et al.* 1988) mainly occur in infertile ponds which are prone to disturbance. According to Taylor *et al.* (1990), the traditional opportunistic type of r strategy (MacArthur & Wilson 1967) performs poorly in impoverished habitats, which are sites with a low mean within-year maximum potential biomass or productivity in the absence of disturbance. Aro wetlands of the inland belong to such sites. Within the r-I

type plant strategy (impoverished and disturbed sites) there is likely to be a greater benefit from resistance to disturbances than from responding opportunistically to gaps (Taylor *et al.* 1990). While true ruderals do not occur in aro wetlands, tree seedlings accompanied by some heath dwarf shrub seedlings act as ruderal-like plants there: the repeated loss of small tree seedlings is the most evident floristic effect of natural disturbances caused by inundation in aro wetlands. Repeated inundation evidently has a marked landscape-level effect on aro wetlands as it keeps them in a treeless state. In a dry period, the relatively bare substratum of aro wetlands is suitable for the germination of seedlings and also partly for dwarf shrubs. The coverages of these species, however, are very small. Tree saplings represent a distinct ecological species group because of their potential for overgrowing other, mostly small-sized species (Urban 2005). In the boreal zone, the mineral soil sites and partly mire sites tend to become stocked in the absence of a disturbance. The hydrological disturbance to tree seedlings is thus an important factor that keeps the aro wetlands open.

Resistance to flooding-induced disturbance is indicated by the fact that the height of the shoots of dominant vascular plant species in different aro wetland communities seems to reflect the depth of flooding (Fig. 7). *Carex lasiocarpa* with longer shoots (69 cm; Toivonen & Lappalainen 1980) occurs at sites that are flooded more deeply than at sites dominated by more low-grown *Rhynchospora fusca* (shoots 15–30 cm long; Hämet-Ahti *et al.* 1998). In the mud flat the duration and depth of flooding are so considerable that the disturbance caused by flooding evidently keeps the site practically devoid of *Carex lasiocarpa* shoots, which occur abundantly around the mud flat i.e. around the lowest site. The maximum height of flood, approximately over 50 cm, about equals the mean length of *C. lasiocarpa*: even total submergence during growing seasons is probable. The long hydrological cycle with a prolonged hydroperiod, with a relatively deep flood, is crucial for the near-lack of *C. lasiocarpa* in mud flats. In general, the *Carex* species in lakes thrive best when there is some fluctuation in water table level and the fluctuation is suitable (Hellsten *et al.* 2006), and

on lakeshores they are typically limited to the water level fluctuation zone (e.g. Hellsten 2001). Typical aapa-mire-centre species are relatively low-grown (*Carex limosa* 10–40 cm high, *C. chordorrhiza* 10–30 cm high; Hämet-Ahti *et al.* 1998) and the flood in them is not as high as in aro wetlands, when the ground surface is used as the reference point (Laitinen *et al.* 2007).

The lack of flooding-induced disturbance in aro wetlands may generate a vegetation succession to forested vegetation. Young *Betula pubescens* and *Pinus sylvestris* shrubs have been found abundant especially in the marginal parts of some aro wetlands. Also several treeless flooded heaths described by Jalas (1953) developed into treed sites during about 50 years. In those cases, a sudden successive development from a temporary wetland to a forest has taken place and the delicate equilibrium supported by the repeated loss of tree seedlings has disappeared. In the sites referred to by Jalas (1953), there has been no ditching. Water level of some lakes has also recently fallen in that area. The reasons for such changes are not evident but may include a slight switch in the groundwater table level caused by large-scale ditching around the sandy formations in which aro wetlands occur (Laitinen *et al.* 2005b). Groundwater aro wetlands might perhaps serve as an indirect environmental indicator for lowered groundwater levels in an areal scale.

### Aspects of pH and nutrient ecology of aro wetlands

Ellenberg's indicator values for soil reaction and nitrogen and the calibration of Ellenberg's reaction on the basis of Finnish fen (mire) data (Tahvanainen *et al.* 2002, Tahvanainen 2004) were used to evaluate the pH and nutrient ecology of aro wetlands. In mires with more stable water regime and thicker peat layer than encountered in the aro wetlands, the water source plays a fundamental role in structuring plant communities in that it regulates the pH and the availability of nutrients. The so called poor–rich gradient in mires correlates with water pH and calcium and covers the greatest part of hydrology-related chemical variation (Sjörs 1952, Sjörs & Gunnarsson 2002). According to Tahvanainen (2004), the

correlation of pH is more consistent than that of calcium, due to the dependence of the latter on regional geochemical conditions. We used the pH correlation of the poor–rich gradient in mires in the calibration of a possibly parallel gradient in the aro wetlands. In line with Ellenberg’s reaction estimate, the pH calibration indicated a relationship with the ordination of aro wetlands. In aro wetlands, surface water (mire water) is not present in the same sense as in the hydrologically more stable mires. Thus, the pH calibration cannot be considered to have indicated a true water pH gradient in the current data. However, it shows that a pH-correlated vegetation pattern, similar to the poor–rich gradient in mires, reappears in the aro wetlands as well. The reason for this may lie in pH and be attributable to the pH of soil or soil pore water. On the other hand, the correlation of pH in the present case is almost exactly coincident with Ellenberg’s value for nitrogen. This is in line with the notion made by Økland *et al.* (2001) that the poor–rich gradient in Fennoscandian mires is connected with the availability of nitrogen along with the pH and mineral gradient. Since no direct measurements are available, there is no ground for any very detailed assessment of the poor–rich gradient in aro wetlands here. In any case, the pattern revealed by the species indicator values indicates that the nutrient availability and pH ought to be taken into account as possible factors structuring vegetation in aro wetlands, alongside with the water level fluctuation and disturbance patterns. The rough similarity of Ellenberg’s reaction and mire water pH calibrations further confirms this conclusion.

In addition, Ellenberg’s indicator value for nitrogen seems to be somehow related to the water table fluctuation pattern within aro wetlands: the surface-water aro wetlands (Polcomaro, Carnigaro), dominated by the seasonal pattern of snow-melt water, have *N* values that are higher than the average *N* value for the two groundwater aro wetland types studied here (Rhyfuaro and mudflat). This may be explained by the concentrations of nitrate and ammonium in relation to corresponding concentrations in snow meltwater: the amount of nitrate in groundwater is only 14% of the amount of nitrate in snow meltwater and the amount of ammonium

in groundwater is only about 4% of the amount of ammonium in snow meltwater in Finland (Soveri *et al.* 2001). Although the hydroperiod of surface-water aro wetlands mainly occurs in spring and not during the growing season, the seasonal flood may dissolve and carry nitrogen from the vegetated catchment more effectively than does the rarer and more prolonged flood of groundwater aro wetlands.

It can be concluded that the aro wetlands are a hydrologic borderline between mires and mineral-soil habitats. Tahvanainen (2005) suggested that “mire” is characterised by the location of water table within the organic soil layer (peat), which allows for the accumulation of organic soil and thus eventually the isolation of the mire surface from the mineral influence of the subsoil. This may be regarded as a good starting point for the concept of mire, as it briefly designates the essential functional character of the mire ecosystem. Towards the “ecological margins”, however, the typical functional features of the particular habitat will become weaker, and in mires (e.g. in sloping fens) there are marginal cases in which the water table fluctuations may well reach the mineral soil within a peat-thickness of 20 cm (Havas 1961): a gradient from hydrologically stable to unstable mires exists. In the latter case the repeated aeration of the peat layer may effect the ceasing of peat growth, and aro wetlands represent the extreme (practically peatless) end of this gradient. The conditions during hydroperiods, on the other hand, make aro communities very distinct e.g. from (mineral soil) forest communities, and the depth and duration characteristics of flooding and duration characteristics of dry periods are important for the occurrence of various aro-wetland communities. The poor–rich gradient as recognised in mires also occurs in aro wetlands but remains to be studied more thoroughly by means of pH measurements. The most essential ecological direction of variation (Tuomikoski 1942, Sjörs 1948) for aro wetlands could be called “flood and desiccation influence” (Laitinen 1990). “Flood” in this connection refers to a flood of about 20 cm or more, and the “desiccation” to the fact that drought is a more direct effect for plants than the depth of water level in the ground. The main influence mechanism of flood and desiccation

is the decrease in species number as a result of natural disturbance. Accordingly, the continuum from mires to aro wetlands clearly appears as a disturbance gradient (e.g. Day *et al.* 1988) rather than a resource gradient (Austin & Smith 1989). The decreasing of species richness, caused by the water level fluctuations, seems to exceed the possible raising impact, caused by the supplementary nutrient effect (Eurola *et al.* 1984, 1995) resulting from flooding.

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## References

- Alalammi, P. (ed.) 1987: Climate. — Atlas of Finland, Folio 131. Nat. Board Survey & Geogr. Soc. Finland, Helsinki.
- Anderberg, M. R. 1973: *Cluster analysis for applications*. — Acad. Press, New York.
- Austin, M. P. & Smith, T. M. 1989: A new model for the continuum concept. — *Vegetatio* 83: 35–47.
- Brinson, M. M. 1993: Changes in the functioning of wetlands along environmental gradients. — *Wetlands* 13: 65–74.
- Cajander, A. K. 1913: Studien über die Moore Finnlands. — *Acta Forest. Fenn.* 2: 1–208.
- Day, R. T., Keddy, P. A., McNeill, J. & Carleton, T. 1988: Fertility and disturbance gradients; a summary model. — *Ecology* 69: 1055–1054.
- De'ath, G. 1999: Extended dissimilarity: a method of robust estimation of ecological distances from high beta diversity data. — *Plant Ecol.* 144: 191–199.
- Dierssen, K. 1982: *Die wichtigsten Pflanzengesellschaften der Moore NE-Europas*. — Ed. Conserv. Jard. Bot. Genève.
- Eurola, S. 1967: Über die Vegetation der Alluvialwiesen im Gebiet der geplanten Stauseen von Lokka und Porttipahta im Finnischen Lappland. — *Aquila Ser. Bot.* 5: 1–119.
- Eurola, S. 1999: Kasvipeitteemme alueellisuus. — *Oulanka Reports* 22: 1–116.
- Eurola, S., Hicks, S. & Kaakinen, E. 1984: Key to Finnish mire types. — In: Moore, P. D. (ed.), *European mires*: 11–117. Acad. Press, London.
- Eurola, S., Huttunen, A. & Kukko-oja, K. 1995: Suokasvillisuusopas. — *Oulanka Reports* 14: 1–85.
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, W., Werner, W. & Paulißen, D. 1992: Zeigerwerte von Pflanzen in Mitteleuropa, ed. 2. — *Scripta Geobot.* 18: 1–258.
- Faith, D. P., Minchin, P. R. & Belbin, L. 1987: Compositional dissimilarity as a robust measure of ecological distance. — *Vegetatio* 69: 57–68.
- Fransson, S. 1972: Mire vegetation in south-western Värmland, Sweden. — *Acta Phytogeogr. Suec.* 57: 1–133. [In Swedish with English summary].
- Gopal, B., Kvet, J., Löffler, H., Masing, V. & Pattern, B. 1990: Definition and classification. — In: Patten, B. C. (ed.), *Wetlands and shallow continental water bodies, vol. 1: Natural and human relationships*: 9–15. The Netherlands, SPB Acad. Publ., The Hague.
- Goslee, S. C., Brooks, R. P. & Cole, C. A. 1997: Plants as indicators of wetland water source. — *Plant Ecol.* 131: 199–206.
- Grime, J. P. 1977: Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. — *Am. Nat.* 111: 1169–1194.
- Grime, J. P. 1979: *Plant strategies and vegetation process*. — John Wiley & Sons, Chichester.
- Grime, J. P., Hodgson, J. G. & Hunt, R. 1988: *Comparative plant ecology. A functional approach to common British species*. — Unwin Hyman, London.
- Grootjans, A. P., Ernst, W. H. O. & Stuyfzand, P. J. 1998: European dune slack: strong interactions of biology, pedogenesis and hydrology. — *Trends Ecol. Evol.* 13: 96–100.
- Hæggestrom, C.-A. & Skytén, R. 1987: Two successional stages of the vegetation in a rock-pool in the Åland Islands, SW Finland. — *Ann. Bot. Fennici* 24: 311–316.
- Hämet-Ahti, L. 1981: The boreal zone and its biotic subdivision. — *Fennia* 159: 69–75.
- Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P. (eds.) 1998: *Retkeilykasvio*, 4 ed. — Finnish Mus. Nat. Hist., Bot. Mus., Helsinki.
- Havas, P. 1961: Vegetation und Ökologie der ostfinnischen Hangmoore. — *Ann. Bot. Soc. Vanamo* 31: 1–188.
- Hellsten, S. 2001: Effects of lake water regulation on aquatic macrophyte stands in northern Finland and options to predict these impacts under varying conditions. — *Acta Bot. Fennica* 171: 1–47.
- Hellsten, S., Keto, A., Suoraniemi, M. & Partanen, S. 2006: Long-term changes in the aquatic vegetation of Lake Pääjärven, southern Finland. — *Verh. Internat. Verein. Limnol.* 29: 1–7.
- Isoviita, P. 1966: Studies on *Sphagnum* L. 1. Nomenclatural revision of the European taxa. — *Ann. Bot. Fennici* 3: 199–264.
- Jacquemart, A.-L., Champluvier, D. & De Sloover, J. 2002: A test of moving and soil-removal restoration techniques in wet heaths of the high Ardenne, Belgium. — *Wetlands* 23: 376–385.
- Jalas, 1953: Rokua. Suunnittelun kansallispuiston kasvillisuus ja kasvisto. — *Silva Fennica* 81: 1–97.
- Kalela, A. 1961: Waldvegetationszonen Finnlands und ihre klimatischen Paralleltypen. — *Arch. Soc. Vanamo* 16 (suppl): 65–83.



- Kalliola, R. 1973: *Suomen kasvimaantiede*. — Werner Söderström, Porvoo.
- Keddy, P. 2000: *Wetland ecology. Principals and conservation*. — Univ. Press, Cambridge.
- Kesel, R. & Urban, K. 1999: Population dynamics of *Gentiana pneumonanthe* and *Rhynchospora fusca* during wet heathland restoration. — *Appl. Veg. Sci.* 2: 149–156.
- Korsman, K., Koistinen, T., Korhonen, J., Wennerström, M., Ekdahl, E., Honkamo, M., Idman, M. & Pukkala, Y. 1997: *Suomen kallioperäkarta 1:1000000*. — Geological survey of Finland, Espoo.
- Kotilainen, M. J. 1958: *Molinia coerulea* (L.) Moench — Siniheinä. — In: Jalas, J. (ed.), *Suuri kasvikirja 1*: 346–348. Otava, Helsinki.
- Laitinen, J. 1990: Periodic moisture fluctuation as a factor affecting mire vegetation. — *Aquilo Ser. Bot.* 28: 45–55.
- Laitinen, J., Rehell, S. & Huttunen, A. 2005a: Vegetation-related hydrotopographic and hydrologic classification for aapa mires (Hirvisuo, Finland). — *Ann. Bot. Fennici* 42: 107–121.
- Laitinen, J., Rehell, S., Huttunen, A. & Eurola, S. 2005b: Aro wetlands: ecology, occurrence and conservation in north-central Finland. — *Suo* 56: 1–17. [In Finnish with English summary].
- Laitinen, J., Rehell, S. & Oksanen, J. 2007: Community and species responses to water level fluctuations, with reference to soil layers in different habitats of mid-boreal mire complexes. — *Plant Ecol.* [In press].
- MacArthur, R. H. & Wilson, E. O. 1967: *The theory of island biogeography*. — Princeton Univ. Press, Princeton, NJ.
- Mäkirinta, U. 1977: *Carex elata*-Vegetation und ihre Gliederung am See Kukkia, Südfinnland. — *Aquilo Ser. Bot.* 15: 22–31.
- Minchin, P. R. 1987: An evaluation of relative robustness of techniques for ecological ordinations. — *Vegetatio* 71: 145–156.
- Moen, A. 1985: Classification of mires for conservation purposes in Norway. — *Aquilo Ser. Bot.* 21: 95–100.
- Moen, A. 1999: *National atlas of Norway: Vegetation*. — Norwegian Mapping Authority, Hønefoss.
- Økland, R. H., Økland, T. & Rydgren, K. 2001: A Scandinavian perspective on ecological gradients in north-west European mires: reply to Wheeler and Proctor. — *J. Ecol.* 89: 481–486.
- Oksanen, J., Kindt, R., Legendre, P. & O'Hara, R. G. 2006: *Vegan: community ecology package. R package version 1.8-2*. — Available on the web at <http://cran.r-project.org/>.
- Pakkala, H. 1986: *Oulunsalon Papinjärven makroskooppisesta pohjaeläimistöstä vuosina 1983–1984*. — Univ. Oulu. Dept. Biology.
- Pennanen, T., Strömmer, R., Markkola, A. M. & Firtze, H. 2001: Microbial and plant community structure across a primary soil gradient. — *Scand. J. Forest Res.* 16: 37–43.
- R Development Core Team 2006: *R: a language and environment for statistical computing*. — R Foundation for Statistical Computing, Vienna, Austria.
- Rørslett, B. 1988: Aquatic weed problems in a hydroelectric river: the R. Otra, Norway. — *Regulated rivers: research and management* 2: 25–37.
- Ruuhijärvi, R. 1960: Über die regionale Einteilung der nordfinnischen Moore. — *Ann. Bot. Soc. Vanamo* 31: 1–360.
- Rydin, H., Snoeijs, P. & Diekmann, M. (eds.) 1999: Swedish plant geography. — *Acta Phytogeogr. Suec.* 84: 1–238.
- Sansen, U. & Koedam, N. 1996: Use of sod cutting for restoration of wet heathlands: revegetation and establishment of typical species in relation to soil conditions. — *J. Veg. Sci.* 7: 483–486.
- Siira, J. 1970: Studies in the ecology of the sea-shore meadows of the Bothnian Bay with special reference to the Liminka area. — *Aquilo Ser. Bot.* 9: 1–109.
- Sjörs, H. 1948: Mire vegetation in Bergslagen, Sweden. — *Acta Phytogeogr. Suec.* 21: 1–299. [In Swedish with English summary].
- Sjörs, H. 1952: On the relation between vegetation and electrolytes in North Swedish mire waters. — *Oikos* 2: 241–258.
- Sjörs, H. & Gunnarsson, U. 2002: Calcium and pH in north and central Swedish mire waters. — *J. Ecol.* 90: 650–657.
- Soveri, J., Mäkinen, R. & Peltonen, K. 2001: *Changes in groundwater levels and quality in Finland in 1975–1999*. — The Finnish Environment 420, Finnish Environment Institute. [In Finnish with English summary].
- Tahvanainen, T. 2004: Water chemistry of mires in relation to the poor–rich vegetation gradient and contrasting geochemical zones of the north-eastern Fennoscandian shield. — *Folia Geobot.* 39: 353–369.
- Tahvanainen, T. 2005: *Diversity of water chemistry and vegetation of mires in the Kainuu region, middle boreal Finland*. — Ph.D. thesis, University of Joensuu.
- Tahvanainen, T., Sallantausta, T., Heikkilä, R. & Tolonen, K. 2002: Spatial variation of mire surface water chemistry and vegetation in northeastern Finland. — *Ann. Bot. Fennici* 39: 235–251.
- Taylor, D. R., Aarssen, L. W. & Loehle, C. 1990: On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. — *Oikos* 58: 239–250.
- Toivonen, H. & Lappalainen, T. 1980: Ecology and production of aquatic macrophytes in the oligotrophic, mesohumic lake Suomunjärvi, eastern Finland. — *Ann. Bot. Fennici* 17: 69–85.
- Tuomikoski, R. 1955: Ruohoisuus ja luhtaisuus. — *Suo* 6: 1–18.
- Ulvinen, T., Syrjänen, K. & Anttila, S. (eds.) 2002: Bryophytes of Finland: distribution, ecology and red list status. — *Finnish Environment* 560: 1–354. [In Finnish with English abstract].
- Urban, K. E. 2005: Oscillating vegetation dynamics in a wet heathland. — *J. Veg. Sci.* 16: 111–120.
- Valpas, A. 1964: Vegetation and flora of some flooded areas in Köyliö (Finland). — *Ann. Bot. Fennici* 1: 67–95.
- Williamson, M. H. 1978: The ordination of incidence data. — *J. Ecol.* 66: 911–920.
- Wilson, S. D. 1991: Plasticity, morphology and disturbance in twelve lakeshore plants. — *Oikos* 62: 292–298.
- Wood, S. N. 2003: Thin plate regression splines. — *J. Roy. Statist. Soc. B* 65: 95–114.