

Botanical vicariance in some mire vegetation between Hokkaido and Europe

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Abstract. - The author studies vicariance phenomena in mire vegetation between Hokkaido (Japan) and Europe. Tables of unpublished data are also shown.

Key-words : vicariance - mires - Hokkaido - biogeography - synusial phytosociology.

Résumé. - L'auteur étudie les phénomènes de vicariances végétales entre les tourbières de Hokkaido (Japon) et de l'Europe. Des tableaux de relevés originaux sont également présentés.

Mots-clés : vicariance - tourbières - Hokkaido - biogéographie - phytosociologie synusiale.

I. INTRODUCTION: VICARIANT AND CORRESPONDING FLORA AND VEGETATION

Deil (1992, 1994) has discussed the use of the "vicariance" concept in floristic and vegetation studies: in idiotaxonomy he speaks of vicariance when two (or more) taxa have a direct ancestor in common, "pseudovicariance" if the species are related *via* a more distant ancestor. The word "vicariance" should therefore indicate a degree of genetic similarity. "Corresponding taxa" are taxa which have the same behaviour in different countries, but which are not genetically related. These concepts may also be applied in vegetation studies. In such cases, two "vicariant syntaxa" should have at least some species in common, whereas two "pseudovicariant syntaxa" would have genera (or even families) in common, but no species. Two "corresponding syntaxa" would occupy the same habitat in two different regions without having any species, nor genera in common. In contrast, classical phytosociologists choose not to distinguish these various differing concepts. Instead they usually use the neologism "geovicariant" (e.g. Géhu & Rivas-Martinez, 1981) or "geosynvicariant" for all forms of corresponding associations regardless of their "genetic affinities". The ideas presented here are based on data gathered

during the field Symposium of the International Mire Conservation Group in the Island of Hokkaido (Japan), in September 1996. The botanical nomenclature follows Ohwi (1965) and Kerguelen (1998), although some infrataxa, not mentioned in these lists, have been added.

II. COMPARING THE FLORA

In comparing the mire flora of Hokkaido with that of Europe we may observe the following:

- some species are common to both areas: *Andromeda polifolia*, *Vaccinium oxycoccus*, *Carex pauciflora*, *Drosera rotundifolia*, *Scheuchzeria palustris*, *Rhynchospora alba*, *Hammarbya paludosa*, *Lycopodiella inundata*, *Calla palustris*, *Menyanthes trifoliata*, *Potentilla palustris*, *Carex limosa*, *Carex curta*, *Juncus filiformis*, *Veronica scutellata*, *Gymnadenia conopsea*, *Ophioglossum vulgatum*, *Triglochin palustre*... ;
- some species are common to both regions, but are represented by different sub-species or variants (true vicariance; Table 1);
- some genera are common to both regions, though represented in the two places by corresponding, rather than closely-related, species (pseudovicariance; Table 2);
- in other cases the family is common but the genera are different (Table 3);
- some taxa which are genetically unrelated occupy the same ecological niche (corresponding taxa; Table 4).

If we study the vegetation, we may recognise the same phenomena:

- some associations are the same in both regions (though only in the case of the bryophytes communities);
- different communities may occur in both areas with some species in common (with the same or different sub-species) and can be considered as vicariant or pseudovicariant communities;
- some communities do occupy the same ecological niche, but without any species in common (corresponding communities); in such cases, the species involved are generally subject to the same environmental and evolutionary pressures and thus often tend to look similar in particular structures, or in overall shape; some examples of these features are presented in the following paragraphs.

It is also worth noting that the architecture of the communities, the dynamic and even the coenotic saturation of communities follow the same biological rules in both areas; for example, both basal and derivate communities, in the sense of Kopecky & Hejny (1974), occur in both regions.

III. METHODS

All the mires and their surroundings have been studied with the methods of synusial phytosociology (Gillet *et al.*, 1991; Gillet, 1998). Synthesis have already shown that it is possible to compare the synusial data with the ones of the classical phytosociology. It is beyond the scope of this paper to give full comparative phytosociological tables of the Japanese and European associations. Phytosociological tables of European mire communities have been published for example in Dierssen (1982, 1996), de Foucault (1984), Oberdorfer *et al.* (1992) and others. Unpublished personal data upon synusial bryophytes communities of the European mire have also been used for comparison. The exact

Table 1.- Vicariant mire flora between Hokkaido and Europe.

Tableau 1.- Flore vicariante des tourbières entre Hokkaido et l'Europe.

EUROPE	HOKKAIDO
<i>Calamagrostis stricta</i> var. <i>stricta</i>	<i>Calamagrostis stricta</i> var. <i>aculeolata</i>
<i>Carex dioica</i> subsp. <i>dioica</i>	<i>Carex dioica</i> subsp. <i>gynocrates</i>
<i>Carex lasiocarpa</i> subsp. <i>lasiocarpa</i>	<i>Carex lasiocarpa</i> subsp. <i>occultans</i>
<i>Empetrum nigrum</i> subsp. <i>hermaphroditum</i>	<i>Empetrum nigrum</i> subsp. <i>japonicum</i>
<i>Epilobium palustre</i> var. <i>palustre</i>	<i>Epilobium palustre</i> var. <i>lavandulaefolium</i>
<i>Eriophorum gracile</i> subsp. <i>gracile</i>	<i>Eriophorum gracile</i> subsp. <i>coreanum</i>
<i>Eriophorum scheuchzeri</i> var. <i>scheuchzeri</i>	<i>Eriophorum scheuchzeri</i> var. <i>tenuifolium</i>
<i>Eriophorum vaginatum</i> subsp. <i>vaginatum</i>	<i>Eriophorum vaginatum</i> subsp. <i>fauriei</i>
<i>Galium trifidum</i> subsp. <i>trifidum</i>	<i>Galium trifidum</i> subsp. <i>columbianum</i> (= var. <i>brevipedunculatum</i>)
<i>Hierochloë odorata</i> var. <i>odorata</i>	<i>Hierochloë odorata</i> var. <i>pubescens</i>
<i>Inula salicina</i> var. <i>salicina</i>	<i>Inula salicina</i> var. <i>asiatica</i>
<i>Juncus arcticus</i> subsp. <i>arcticus</i>	<i>Juncus arcticus</i> subsp. <i>sitchensis</i>
<i>Lathyrus palustris</i> subsp. <i>palustris</i>	<i>Lathyrus palustris</i> subsp. <i>pilosus</i>
<i>Ledum palustre</i> subsp. <i>palustre</i>	<i>Ledum palustre</i> subsp. <i>diversipilosum</i>
<i>Myrica gale</i> var. <i>gale</i>	<i>Myrica gale</i> var. <i>tomentosa</i>
<i>Parnassia palustris</i> var. <i>palustris</i>	<i>Parnassia palustris</i> var. <i>multisetata</i>
<i>Pinguicula vulgaris</i> subsp. <i>vulgaris</i>	<i>Pinguicula vulgaris</i> subsp. <i>macroceras</i>

Table 2.- Pseudovicariant mire flora between Hokkaido and Europe.

Tableau 2.- Flore pseudovicariante des tourbières entre Hokkaido et l'Europe.

EUROPE	HOKKAIDO
<i>Alnus glutinosa</i>	<i>Alnus japonica</i>
<i>Gentiana pneumonanthe</i>	<i>Gentiana triflora</i>
<i>Iris sibirica</i>	<i>Iris setosa</i>
<i>Lobelia urens</i>	<i>Lobelia sessilifolia</i>
<i>Narthecium ossifragum</i>	<i>Narthecium asiaticum</i>
<i>Sium latifolium</i>	<i>Sium suave</i>
<i>Spiranthes aestivalis</i>	<i>Spiranthes sinensis</i>
<i>Swertia perennis</i>	<i>Swertia cuspidata</i>
<i>Thelypteris palustris</i>	<i>Thelypteris japonica</i>
<i>Tofieldia calyculata</i>	<i>Tofieldia japonica</i>

Table 3.- Pseudovicariant genus between Hokkaido and Europe.

Tableau 3.- Genres pseudovicariants des tourbières entre Hokkaido et l'Europe.

EUROPE	HOKKAIDO
<i>Molinia caerulea</i>	<i>Moliniopsis japonica</i>
<i>Hypericum elodes</i>	<i>Triadenum japonicum</i>
<i>Liparis loeselii</i>	<i>Platanthera tipuloides</i>

Table 4.- Corresponding mire idiotaxa between Hokkaido and Europe.

Tableau 4.- Idiotaxons correspondants des tourbières entre Hokkaido et l'Europe.

EUROPE	HOKKAIDO
<i>Salix cinerea</i>	<i>Hydrangea paniculata</i>
<i>Dryopteris carthusiana</i> var. <i>elevata</i>	<i>Osmunda asiatica</i>
<i>Narthecium ossifragum</i>	<i>Pogonia japonica</i>

meaning and taxonomical situation of the European units mentioned in the phytosociological tables may be understood by comparing the data given in Julve (1997, 1998a, 1998b). For all the tables, are given the relevé date (year, month, day), the relevé author, the type of synusia (see Julve, 1988, 1999; Gillet, 1998), the cover and the mean vegetative height of vegetation.

During the study, all the relevés have been done using the synusial approach; this is indicated in the tables legends by the sign σ , followed by the dominant biological type (see Julve, 1999, for a short description of them, as used in synusial approach). The criteria used to recognize synusiae on the field are the following: floristical homogeneity (taking into account the ecophens of plants), spatial homogeneity (vital space in three dimension), homogeneity of biological types, phenological homogeneity, dynamic homogeneity, homogeneity of soil and mesoclimate, morphological homogeneity. None of these criteria are sufficient alone, but a combination of at least some of them is used to delimit synusiae. After the analytical field stage (where relevés are done), the synthetical stage is reached in order to sort out the tables of elementary syntaxa (*sensu* de Foucault, 1984), using floristical criteria. The elementary syntaxa, which have ecological attributes, are then compared to the bibliography in order to establish their hierarchical rank (association, subassociation, geographical race, dynamic stage...). This procedure may also reveal some characteristic species (faithful species), which may later define the syntaxa, although it has been recognized at first by a floristic combination based on constancy.

The mires of Hokkaido show a surface pattern which fit well within the microform system described for Europe by Lindsay *et al.* (1985, 1988, 1995). In this system the terrestrial zones (T) consist of: T3 hummock, normally the highest element in the pattern, bryophyte formed (*Sphagnum capillifolium*, *S. imbricatum*, *S. fuscum*, *Racomitrium lanuginosum*..., sometimes some lichenes on top), 20 cm to 1 m above the water level; T2 high ridge, the general level of many mires surfaces (with *S. rubellum*, *S. magellanicum*..., but also often dominance of *Calluna vulgaris*), particularly outside pool system, 10-20 cm above the water table, occurring at the middle of hummocks slope or as narrow ridges between pools, or as wide expanses of drier vegetation within pools systems; T1 low ridge (lawn *sensu* Sjörs, 1948), common on mire areas which are free from damage, occurring at the base of hummock (far less dominated by dwarf shrubs, with *S. magellanicum*, *S. papillosum*, *S. fallax*, *S. angustifolium*, *S. tenellum*...), 1-10 cm above the mean water table.

The aquatic zones (A) consist of: A1 *Sphagnum* hollows of dense aquatic *Sphagna* (*S. cuspidatum*...) carpet (*sensu* Sjörs, 1948), 0-10 cm below the mean water table; A2 mud-bottom hollows (Sjörs, 1948) are dominated by a relatively solid bare peat base, but with some sparse aquatic *Sphagna*, 5-20 cm below the mean water surface; A3 drought sensitive pools, an area of open water with unconsolidated peat base, flooded much of the time but may dry up in drought conditions, 20-50 cm below the mean water table; A4 permanent pool, an area of open water sufficiently deep to remain always flooded, 1-4 m deep.

In addition, three others types have been described: TA2 erosion gullies, resembling mud-bottom hollows but with flowing water; T4 peat hagg, associated with erosion, 1-2 m above the mean water table; T5 peat mound, 1-3 m above mean water table, mostly seen in *palsa* mires.

IV. THE MIRES AND THEIR SURROUNDINGS

A. Lakes shores (Table 5)

Along the shores of the lakes in Hokkaido, we may find some plant communities which grow in the same ecological conditions as those found in Europe, often also displaying the same structural features:

* The community *Zizanio latifoliae* - *Schoenoplectetum lacustris* is the vicariant of our European *Typho angustifoliae* - *Schoenoplectetum lacustris* Passarge 1964. Like this one, it occurs on lake margins directly upon gravel or sandy soils and may tolerate relatively deep water.

* The *Thelypterido nipponicae* - *Phragmitetum australis* is an exact vicariant of the European *Thelypterido palustris* - *Phragmitetum australis* Kuiper 1957 em. Segal & Westhoff in Westhoff & den Held 1969. Both communities are found on neutrophilous peat which accumulates in topogenous or fluviogenous conditions.

* The community with *Calamagrostis langsdorffii* (described in Tachibana *et al.*, 1996, as *Phragmites australis* - *Calamagrostis langsdorffii* comm.) is a pseudovicariant of our European community with *Calamagrostis canescens* (*Peucedano palustris* - *Calamagrostietum canescentis* Korneck 1978).

Table 5.- Lakes shores.

Tableau 5.- Bords des lacs.

1. *Zizania latifoliae* - *Schoenoplectetum lacustris* ass. nov.; Lake Takkobu, Kushiro mire (96/9/3), Ph. Julve, σH: 90%, 2,30 m.
2. *Thelypterido nipponicae* - *Phragmitetum australis* ass. nov.; Lake Takkobu, Kushiro mire (96/9/3), Ph. Julve, σH: 90%, 1,80 m.
3. community with *Calamagrostis langsdorffii*; Onnenai, Kushiro mire (96/9/4), Ph. Julve, σH: 80%, 1,50 m.

	1	2	3
<i>Phragmiti australis</i> - <i>Caricetea elatae</i>			
<i>Schoenoplectus lacustris</i>	1		
<i>Zizania latifolia</i>	2		
<i>Lythrum salicaria</i>	1		
<i>Typha latifolia</i>	+		
<i>Phragmites australis</i>	4	5	3
<i>Sium suave</i>	1	1	2
<i>Cicuta virosa</i>	(+)	1	2
<i>Equisetum fluviatile</i>			+
<i>Thelypteris nipponica</i>	2		
<i>Lysimachia thyrsiflora</i>	1		
<i>Calamagrostis langsdorffii</i>			1
<i>Carex</i> sp. "elongata shape"			3
companions species			
<i>Lobelia sessilifolia</i>		+	+
<i>Rumex cf. gmelinii</i>			+

Table 6, Tableau 6.- *Eriophoro gracilis* subsp. *coreani* - *Caricetum lasiocarpae* subsp. *occultans* ass. nov.

- 1: Kiritappu (96/9/1), Ph. Julve, σh; 2: Lake Akanuma, Kushiro mire (96/9/4), Ph. Julve, σh; 3: Lake Akanuma, Kushiro mire (96/9/4), Ph. Julve, σh; phytocenotic complex with a sphagnum synusia; 4: Onnenai, Kushiro mire (96/9/4), Ph. Julve, σh: 60%, 0,60 m; 5: Akkeshi area (96/9/4), Ph. Julve, σh: 90%, 1,00 m; 6: Bikanbeushi (96/9/1), Ph. Julve, σh: 70%, 0,50 m, water depth: 20 cm.

	1	2	3	4	5	6
<i>Potentillo palustris</i> - <i>Menyanthenenea trifoliatae</i>						
<i>Carex lasiocarpa</i> subsp. <i>occultans</i>	X	X	4	5	4	4
<i>Menyanthes trifoliata</i>	X	X	1		1	2
<i>Calamagrostis langsdorffii</i>	X	X	1	1	1	
<i>Eriophoro gracile</i> subsp. <i>coreanum</i>		X		1	1	
<i>Potentilla palustris</i>	X	X				
<i>Carex limosa</i>	X	X				
<i>Rhynchospora alba</i>						2
<i>Drosera rotundifolia</i>						+
<i>Eriocaulon</i> sp.						+
<i>Moliniopsienea japonicae</i>						
<i>Lobelia sessilifolia</i>	X		2	2	+	
<i>Iris setosa</i>		X	3	2		
<i>Myrica gale</i> var. <i>tomentosa</i>					2	2
<i>Hosta rectifolia</i>					1	
<i>Sanguisorba tenuifolia</i> var. <i>alba</i>					+	
<i>Parnassia palustris</i> var. <i>multisetata</i>					+	
<i>Spiranthes sinensis</i>					+	
<i>Triadenum japonicum</i>						+
<i>Carex</i> sp.			+			
<i>Phragmiti australis</i> - <i>Caricetea elatae</i>						
<i>Equisetum fluviatile</i>	X	X				
<i>Sium suave</i>		X	2			
<i>Cicuta virosa</i>	X	X	1	2		
<i>Phragmites australis</i>			1	1	2	3
<i>Thelypteris nipponica</i>				1	2	
companions species						
<i>Rubia jesoensis</i>				1		
<i>Equisetum palustre</i>					1	

* A community with *Eleocharis interseta* (= *E. palustris* subsp. *palustris* ?) has also often been seen on the gravelous shore lakes with a silt matrix. It reminds clearly of the communities with *Eleocharis palustris* on mineral soil, or with *Eleocharis mamillata* on organic soils, that we may find in Europe, in the same ecological conditions, at the same topographical level.

B. Floating mats (Table 6)

* A community with *Carex lyngbyei* & *Carex rhynchophysa* has been described in the Japanese bibliography (for example Suzuki, 1975). This community was not studied during the fieldwork but should occur in Lake Rausu and Kiritappu mire (Tachibana *et al.*, 1996).

* The *Eriophoro gracilis* subsp. *coreani* - *Caricetum lasiocarpae* subsp. *occultans*, described in Japanese literature (Numata, 1974; Numata *et al.*, 1975; Tachibana *et al.*, 1996) as *Myrica gale* var. *tomentosa* - *Carex lasiocarpa* subsp. *occultans* comm. is a vicariant of the European *Eriophoro gracilis* - *Caricetum lasiocarpae* Vollmar 1947 and occurs like this one on floatings mats in neutrophilous conditions, during the initial stages of mire terrestrialization in limnogenous mires.

* In some places, we saw a community with a blueish carex (*Carex pseudocuraica*), which occupies shallow depression in fens areas. The shape of this *Carex* reminds of the European *Carex disticha*, and the topographical occurrence is the same but the Japanese stands seems more peaty, compared to the European ones.

C. Lawns (Table 7)

Lawns are well spread in the mires of Hokkaido, corresponding with the T1 level in Lindsay's terminology. We may recognise:

* A *Carici oligospermae* - *Eriophoretum vaginati*, which should be the equal of our European community with *Eriophorum vaginatum*, occurring on pertubated mires, often mineralized at surface.

* The *Geo pentapetali* - *Caricetum midden-dorffii* should be an equivalent of some of our Scandinavian or Alpine communities but do occur on natural mire places with a small geotrophic influence, for example like the strings of Aapa mires. This community has only be seen in the highest mire of Lake Rausu. A mire with very subarctic climatic conditions has have shown the snowbeds seen there in September !

* For the bryophytes, the Japanese lawns are characterized by *Sphagnum papillosum*-*Sphagnum fallax* and *Sphagnum magellanicum*-*Sphagnum rubellum* communities, which seem to be the same as in Europe. On higher altitude, like around Lake Rausu, a community with *Sphagnum russowii* and *Sphagnum teres* has been found, but our observations are too scattered to make a better comparison with the vicariant bryophytes community of Europe (which could be the same !). Another bryophyte community with *Sphagnum imbricatum*-*Sphagnum subfulvum* is described by Tachibana *et al.* (1996), from the Kiritappu mire. This last one could occur in Europe in Boreal-Oceanic conditions, but is now rarely found.

Table 7, Tableau 7.

- 1, 2: *Carici oligospermae* - *Eriophoretum vaginati* ass. nov.; 1: Kiritappu (96/9/1), Ph. Julve, sh: 70%, 0,60 m; 2: Cape Ochiishi (96/8/29), Ph. Julve, sh: 90%, 0,50 m; phytocoenotic complex with a moss synusia: *Sphagnum fuscum*, *Polytrichum strictum*.
3, 4: *Geo pentapetali* - *Caricetum midden-dorffii* ass. nov.; 3: Lake Rausu, 6 relevés from excursion's guide (sheet distributed on the field: rel. n° 14 to 19); phytocoenotic complex with a moss synusia: *Sphagnum magellanicum* V, *Sphagnum papillosum* IV, *Sphagnum* sp. I, *Polytrichum* sp. I; 4: Lake Rausu (96/9/5), Ph. Julve, sh: 70%, 0,40 m; phytocoenotic complex with a moss synusia: *Sphagnum magellanicum*, *Sphagnum teres*, *Sphagnum russowii*, *Aulacomnium palustre*.

	1	2	3	4
<i>Moliniopsienea japonicae</i> (char. and diff.)				
<i>Moliniopsis japonica</i>	X	4		1
<i>Myrica gale</i> var. <i>tomentosa</i>	X	2		
<i>Carex oligosperma</i>	X	1		
<i>Solidago virgaurea</i> var. <i>leiocarpa</i>	X	1		
<i>Eriophorum vaginatum</i>	X	3	V	
<i>Sanguisorba tenuifolia</i> var. <i>alba</i>	X	2	V	+
<i>Drosera rotundifolia</i>		+	III	2
<i>Carex pauciflora</i>			III	2
<i>Carex midden-dorffii</i>			V	4
<i>Geum pentapetalum</i>			V	2
<i>Carex michauxiana</i>			I	2
<i>Coptis trifolia</i>			V	1
<i>Hosta rectifolia</i>			V	+
<i>Tilingia ajanensis</i>			IV	1
<i>Parnassia palustris</i> var. <i>multiset</i>			III	1
<i>Platanthera tipuloides</i>			III	+
<i>Trientalis europaea</i> subsp. <i>arctica</i>			V	
<i>Iris setosa</i>			II	
<i>Ledetalia palustris</i>				
<i>Vaccinium oxycoccus</i>			V	2
<i>Ledum palustre</i> subsp. <i>diversipilosum</i>			+	
companions species				
<i>Ligularia hodgsonii</i>				+
<i>Eleocharis margaritacea</i>				+
<i>Calamagrostis langsdorffii</i>	X		III	
<i>Hemerocallis flava</i> var. <i>yezoensis</i>			II	
<i>Sasa senanensis</i>			IV	

D. Hummocks (Table 8)

Like European mire, Japanese mire may exhibit a surface pattern with hollows and hummocks.

* The *Rhododendro parvifolii* - *Chamaedaphnetum calyculatae* is an exact vicariant of the European *Chamaedaphno calyculatae* - *Ledetum palustris* subsp. *palustris* Korotkov 1986.

Table 8, Tableau 8.

1-7: *Rhododendro parvifolii* - *Chamaedaphnetum calyculatae* ass. nov.; 1: Akkeshi area (96/9/4), Ph. Julve, σ ch: 2; Akkeshi area (96/9/4), Ph. Julve, σ ch: 90%, 0,10 m; 3: Akkeshi area (96/9/4), Ph. Julve, σ ch: 80%, 0,10 m; 4: Akkeshi area (96/9/4), Ph. Julve, σ ch: 80%, 0,15 m; 5: Lake Akanuma, Kushiro mire (96/9/4), Ph. Julve, σ ch: 80%, 0,10 m; 6: Cape Ochiishi (96/8/29), Ph. Julve, σ ch: 30%, 0,15 m; 7: Bikanbeushi mire, 6 relevés from Field Guide (p. 45, table 1, col. A1).

10-11: *Coptido trifoliae* - *Caricetum pauciflorae* ass. nov. (transition with the lawns); 8: Shibetsu mire, 21 relevés from Field Guide (p. 16, table 1, col. A1); 9: Shibetsu mire (96/8/29), Ph. Julve, σ ch; 10: Shibetsu mire (96/8/29), Ph. Julve, σ ch: 80%, 0,10 m; 11: coming back from Lake Rausu, first mire (96/9/5), Ph. Julve, σ ch: 70%, 0,20 m.

	1	2	3	4	5	6	7	10	8	9	11
<i>Ledetalia palustris</i> (char. and diff.)											
<i>Ledum palustre</i> subsp. <i>diversipilosum</i>	X	2	3	2	2	2	V	V	X	4	2
<i>Empetrum nigrum</i> subsp. <i>japonicum</i>	X	3	3	2	3	(1)	V	V	X	3	
<i>Vaccinium oxycoccos</i>	X	3		1	2			III	X	2	3
<i>Vaccinium microcarpum</i>			1				V	V			
<i>Andromeda polifolia</i>		1			1			I			1
<i>Chamaedaphne calyculata</i>	X	1	2	2	2	2	V				
<i>Rhododendron parvifolium</i>						I					
<i>Vaccinium vitis-idaea</i> subsp. <i>minus</i>						I		V	X	1	1
<i>Carex pauciflora</i>								IV	X	2	2
<i>Cornus suecica</i>								IV	X	1	
<i>Lycopodium obscurum</i> fo. <i>strictum</i>								I			
<i>Moliniopsisjapónica japonicae</i> (char. and diff.)											
<i>Scheuchzeria palustris</i>	X	1									
<i>Pogonia japonica</i>	X										
<i>Carex lasiocarpa</i> subsp. <i>occultans</i>	X ^o										
<i>Trientalis europaea</i> subsp. <i>arctica</i>	X							I			
<i>Solidago virgaurea</i> var. <i>leiocarpa</i>	X						IV	II			
<i>Carex middendorffii</i>	X	1	2	2	2		V	V	X	2	
<i>Myrica gale</i> var. <i>tomentosa</i>	X		2	2	1	3	V	I	X		
<i>Drosera rotundifolia</i>	X	1	+		+	1	III	V	X	1	
<i>Eriophorum vaginatum</i>		2					V	V		+	3
<i>Coptis trifolia</i>								V	X	2	2
<i>Moliniopsis japonica</i>				+	1	+		II	X		1 ^o
<i>Sanguisorba tenuifolia</i> var. <i>alba</i>					1	+	III				1 ^o
<i>Hosta rectifolia</i>			1 ^o	+			I				
<i>Calamagrostis stricta</i> var. <i>aculeolata</i>							V	V			
<i>Osmunda asiatica</i>							I	I			
<i>Platanthera tipuloides</i>								I			
<i>Parnassia palustris</i> var. <i>multisetata</i>											1
<i>Geum pentapetalum</i>											1
<i>Iris setosa</i>											1
<i>Carex oligosperma</i>						+					
companions species											
<i>Phragmites australis</i>		+									
<i>Equisetum palustre</i>			1								
<i>Thelypteris nipponica</i>							1				
<i>Anemone debilis</i>								1			

Table 9, Tableau 9.- *Mylio anomalae* - *Sphagnetum fusci* ass. nov. (all relevés are σ M).
phytocoenotic complexes with the relevés of table 8, same locations.
complexes phytocénotiques avec les relevés du tableau 8, mêmes lieux.

	8	1	5	2	4	7	11	9	3	8	6
<i>Sphagnum fuscum</i>	V	X	4	5	2	V	X	X	X	X	X
<i>Polytrichum strictum</i> (= <i>juniperinum</i> subsp. <i>strictum</i>)	V	X	2	2	3	V	X	X	X	X	X
<i>Sphagnum magellanicum</i>	II	X	1	+	3	I	X	X			
<i>Sphagnum papillosum</i>		X	2								
<i>Sphagnum palustre</i>			+								
<i>Sphagnum capillifolium</i> (= <i>nemoreum</i>)	I										
<i>Dicranum</i> sp.	I										
<i>Sphagnum flexuosum</i> (= <i>amblyphyllum</i>)	I										
<i>Pleurozium schreberi</i>	I										
<i>Jungermannia</i> sp.	I										
<i>Mylia anomala</i>								X	X		

It occurs on the driest part of the hummocks (T3 in Lindsay's terminology) and has a boreal-oceanic character.

* The *Coptido trifoliae* - *Caricetum pauciflorae* (transition with the lawns), occurs somewhat closer to the mire water-table (T2 in Lindsay's terminology). It is a vicariant of European *Carex pauciflora* - communities.

* The *Mylio anomalae* - *Sphagnetum fusci* ass. nov. has exactly the same floristic composition as in Europe (Table 9). The association also has the same ecology in Japan, being one of the most effective producer of peat in the bogs. From the bibliography is reported a community with *Sphagnum capillifolium* (= *S. nemoreum*), which we did not clearly see on the field, and which seems rare regionally, but it should be comparable to the European one, the *Ptilidio ciliaris* - *Sphagnetum capillifolii* (Koch 1928) Julve 1993 ex 1999.

E. Hollows (Table 10)

Following the literature, the hollows vegetation seems much more diversified in Japan compare to Europe. This is seen for example by the great richness in species of genus like *Eriocaulon* or *Utricularia* which may even develop terrestrial species in Japan. These units do occupy the A1 level in Lindsay's terminology.

* The *Rhynchosporo fauriei* - *Caricetum limosae* Miyawaki & Fujiwara 1970 is the vicariant association of the *Drosero longifoliae* - *Rhynchosporium albae* (Koch 1926) Klika 1935 of subatlantic Europe and do participate like this one to the regeneration processes in bogs areas.

* The *Utriculario yakusimensis* - *Eriocaulum sikokiani* Fujiwara 1979 seems to have no equivalent community in Europe, as our *Utricularia* species are more aquatic, while *Eriocaulon* is represented in Europe by only one aquatic species : *Eriocaulon septangulare*. Perhaps could we compare with our European *Eleocharis acicularis* communities: *Eleocharitetum acicularis* (Baumann 1911) Koch 1926, *Littorello uniflorae* - *Eleocharitetum acicularis* (Chouard 1924) Malcuit 1928, but, in Europe, these associations occur in the shore of oligotrophic lakes and are not typically found in the mire expanse, like the case we saw in Kushiro mire. Here, the community did occur on a disturbed mud-bottom square, in the mire expanse. The only way to solve this comparison question would be to better know the corresponding japanese communities of our European *Littorelletea uniflorae* (which could perhaps include the *Utricularion intermedio-minoris* ?).

Table 10, Tableau 10.

1 à 5: *Rhynchospora fauriei* - *Caricetum limosae* Miyawaki & Fujiwara 1970; 1: Bikanbeushi mire, 7 relevés from Field Guide (p. 46, table 2); 2: Lake Akanuma, Kushiro mire (96/9/4), Ph. Julve, sh: 0,20 m, 20%; phytocoenotic complex with a *Sphagnum papillosum* synusia; 3: Akkeshi area (96/9/2), Ph. Julve, sh; 4: Lake Akanuma, Kushiro mire (96/9/4), Ph. Julve, sh; 5: Lake Rausu (96/9/5), Ph. Julve, sh: 40%, 0,25 m, water depth: 20-30 cm.
6: *Utricularia yakusimensis* - *Eriocaulum sikokiani* Fujiwara 1979; Lake Akanuma, Kushiro mire (96/9/4), Ph. Julve, sh: 70%, 0,10 m.

	1	2	3	4	5	6
<i>Eleocharis acicularis</i> var. <i>longiseta</i>						4
<i>Utricularia yakusimensis</i>						2
<i>Scirpus juncoides</i>						1
<i>Eriocaulon kusiroense</i>						1
<i>Eleocharis wichurae</i>						+
<i>Potentillo palustris</i> - <i>Menyanthes trifoliatae</i>						
<i>Rhynchospora alba</i>	V	2	X	X	(+)	2
<i>Drosera rotundifolia</i>	III	1			2	1
<i>Scheuchzeria palustris</i>	III	+	X		2	
<i>Carex limosa</i>	III	4	X	X	4	
<i>Menyanthes trifoliata</i>				X	1	
<i>Hammarbya paludosa</i>		(+)				
<i>Moliniopsisenea japonicae</i>						
<i>Myrica gale</i> var. <i>tomentosa</i>	III	1°				
<i>Hosta rectifolia</i>	IV	+°				
<i>Pogonia japonica</i>	II	+				
<i>Calamagrostis stricta</i> var. <i>aculeolata</i>	III					
<i>Carex middendorffii</i>	III					
<i>Lobelia sessilifolia</i>	III					
<i>Sanguisorba tenuifolia</i> var. <i>alba</i>	III					
<i>Iris laevigata</i>	II					
<i>Carex lasiocarpa</i> subsp. <i>occultans</i>	II					
<i>Solidago virgaurea</i> var. <i>leiocarpa</i>	II					
<i>Osmunda asiatica</i>	II					
<i>Parnassia palustris</i>	I					
<i>Viola blandaeformis</i> var. <i>pilosa</i>	I					
<i>Coptis trifolia</i>		+°				
<i>Moliniopsis japonica</i>		+°				
<i>Iris setosa</i>				X		
<i>Lysichiton camtschatcense</i>					+	
<i>Ledetalia palustris</i>						
<i>Andromeda polifolia</i>	I	2				
<i>Vaccinium oxycoccus</i> (<i>microcarpum</i> *)	I*	+				
<i>Trientalis europaea</i> subsp. <i>arctica</i>	I	+				
<i>Empetrum nigrum</i> subsp. <i>japonicum</i>	II					
<i>Chamaedaphne calyculata</i>	I					
<i>Ledum palustre</i> subsp. <i>diversipilosum</i>	I					
companions						
<i>Phragmites australis</i>	III			X		
<i>Utricularia intermedia</i>	III					
<i>Equisetum palustre</i>	III					
<i>Thelypteris nipponica</i>	I					
<i>Equisetum fluviatile</i>				X		

* Like in Europe, the hollows vascular plants may occur in phytocoenotic complex with a *Sphagnum cuspidatum* bryophyte community which has been seen but not studied.

F. Pools and mire lakes

* We did not study many pools during the field symposium, even if we passed near some of them. The following is very interesting, being dominated by *Brasenia schreberi*, a formerly subcosmopolitan species only found at fossil stage in Europe:

Brasenia schreberi 4, *Potamogeton fryeri* 2, *Nuphar pumila* 1, *Utricularia intermedia* 1 (Bekanbeushi, 96/9/1), Ph. Julve, σ h: 90%, water depth: 1,50 m).

* We also saw some aquatic *Utricularia* communities, corresponding with the European *Utricularion intermedio - minoris* (Müller & Görs 1960) Julve 1993 prov. and occurring in the same ecological situation (A2 in Lindsay's terminology).

* The mire lakes are often colonized, like in northern or alpine Europe, by small populations of *Nuphar pumila*, as we saw in Lake Akanuma.

* Floating populations of *Trapa japonica* are also common, differing of the European *Trapa natans* community in the ecology, this last one being much more thermophilous and being not found in mires.

G. Lags (wet margins)

We did not had much time to look at the mires margins, but there seems to exist sometimes a "lagg" zone, like in European raised bogs. This zone is also occupied by hygrophilous fen communities, which are stable and should not be mixed with the floating mat communities of the primary dynamic, mostly transitional.

* The community with *Lysichiton camtschatcense* has no clear floristical equivalent in Europe, but looks like our *Calletum palustris* (Osvald 1923) Vanden Berghen 1952 :

Moliniopsienea japonicae : *Carex middendorffii* 3, *Moliniopsis japonica* 3, *Potentilla palustris* 2, *Galium trifidum* subsp. *columbianum* 1, *Lysichiton camtschatcense* 1, *Sanguisorba tenuifolia* var. *alba* 1,

companions species : *Phragmites australis* 2, *Lysimachia thyrsiflora* 1
(Lake Rausu, 96/9/5), Ph. Julve, σ h: 90%, 0,60 m).

H. Megaphorbs (hygrophilous margin)

* A community with *Carex cespitosa* & *Carex thunbergii* has been reported in the bibliography (Numata, 1974; Numata *et al.*, 1975), but has not been seen on the field.

* A community with *Lobelia sessilifolia* & *Osmunda asiatica* occurs typically along the ditches in Shibetsu mire, a position where megaphorbs communities occur in Europe. The megaphorbs are better developed on mineral soil and are found only sporadically on peat, in disturbed places, or along drainage ditches.

I. Heaths (dry margin)

In the volcanic zone of Akan National Park, we saw a moor heathland landscape with a chamaephytic community, 55 cm high. As in Europe, this heathland shows the relationship between terminal stages of mire dynamic and heaths, exhibiting such species commonly found in the mire like : *Ledum palustre* subsp. *diversipilosum*, *Empetrum nigrum* subsp. *japonicum*, *Osmunda asiatica* (= *Osmundastrum cinnamomeum*), but also typical heath species like *Vaccinium vitis-idaea*, *Cornus suecica*, *Lycopodium obscurum*... locally accompanied by a *Poaceae* : *Miscanthus sinensis*. This heathland community clearly belongs to the same phytosociological class as in Europe (*Calluno vulgaris* - *Vaccinietea myrtilli* (Braun-Blanquet, Sissingh & Vlieger 1939) de Foucault 1990).

J. Shrubs associations

* In most of the mire, we have seen a shrub community with *Hydrangea paniculata*, *Sorbus sambucifolia*, *Alnus japonica* juv., *Betula platyphylla* var. *japonica* juv. (juv. means juveniles stages of bigger trees). This scrub seems to replace in Japan the communities with *Salix cinerea* or *Salix aurita* of European mires, while the presence of juveniles of an

Alnus and a *Betula* suggests the possibility of a “*Betulo - Alnetum*”, typical mire tree association, vicariant of the European *Betulo albae* subsp. *albae* - *Alnetum glutinosae* Julve & Gillet 1994 (*B. alba* = *B. pubescens* !).

* In the volcanic zone of Akan National Park, a *Pinus pumila* small scrub (2 m) occurs in phytocoenotic complexes with the earlier described heath. With the pine, we may found here *Salix sacchalinensis*, *Hydrangea paniculata*, *Betula platyphylla* juv.

V. THE TREES ASSOCIATIONS OF THE FORESTS

Mostly, true forest communities are developed on mineral soils, but some of the trees may also occur in mires.

* In Ochiishi Cape, on peat, but also in Akan national Park, especially in the high volcanic zone, some forest may be seen, sending some of their tree species in the heathlands and mires around. A high tree community (σA in synusial terminology) with *Picea glehnii* & *Abies sacchalinensis* is recognizable. It is poor in species and sometimes accompanied by lowland species like *Quercus mongolica* var. *grosseserrata* (= *Q. crispula*). This community remind of course the subalpine European one with *Picea abies* & *Abies alba* (*Abieti albae* - *Piceetum abietis* (Oberdorfer 1950) Julve 1993 prov.).

* In the same area a low-tree community (σa in synusial terminology) is made by nomad pioneer trees like *Betula platyphylla* (a vicariant of the European *Betula pendula*).

* In the alluvial valleys, a community with *Alnus japonica* & *Fraxinus mandshurica* var. *japonica*, where also occur *Pterocarya rhoifolia*, *Ulmus laciniata*, *Acer mono*, is the exact vicariant of the European *Fraxino excelsioris* - *Alnetum glutinosae* (Matuszkiewicz 1952) Julve 1993 ex de Foucault 1994.

* On the slope of the surroundings of Lake Mashu (in Akan National Park) we saw a typical community with *Acer mono* & *Fraxinus mandshurica* var. *japonica*, vicariant of our *Aceri pseudoplatani* - *Fraxinetum excelsioris* (Koch 1926) Gillet 1986. Like this last one, the understorey of the forest is occupied by a megaphorb community, 1 m high, with *Filipendula yezoensis*, *Aconitum yamazakii*, *Eupatorium chinense*, *Cirsium kamtschaticum*, *Senecio cannabifolium*, *Calamagrostis epigeijs* and *Sasa chartacea*. The simple list of the represented genus (except *Sasa* !) clearly exhibits the relationships with the European mountainous megaphorbs (a typical vicariance case).

* The collinean belt of Hokkaido shows a deciduous tree community (*Quercus mongolica* var. *grosseserrata* - *Tilia maximowicziana* comm.), which may dominate the rare forests patches. We may find in it the following species, compared with European ones (Table 11).

This remarkably exact vicariance between arboreal communities of deciduous forest in temperate areas was observed in the vicinity of Kushiro mire. Not only are the same genera represented by vicariant species, but also the equivalent number of species per genera and even the dominance ratio and the role in the dynamic and architecture of each species in these forests seem to be the same. As no older forests were examined, we did

Table 11.- Pseudovicariant tree species of the planar mesophilous forests between Western Europe and Hokkaido.

Tableau 11.- Arbres pseudovicariants des forêts méso-philés planitiaires en Europe occidentale et à Hokkaido.

EUROPE	HOKKAIDO
<i>Quercus robur</i>	<i>Quercus mongolica</i> var. <i>grosseserrata</i> (= <i>Q. crispula</i>)
<i>Carpinus betulus</i>	<i>Carpinus cordata</i>
<i>Prunus avium</i>	<i>Prunus sargentii</i>
<i>Acer pseudoplatanus</i>	<i>Acer mono</i>
<i>Tilia cordata</i>	<i>Tilia japonica</i>
<i>Betula pendula</i>	<i>Betula platyphylla</i> var. <i>japonica</i>
<i>Fagus sylvatica</i>	<i>Fagus crenata</i>

not find on the field the Japanese beech *Fagus crenata*, but it would probably occupy the same niche as the European *Fagus sylvatica*.

We may also point out that not only species and community have their counterpart between Europe and Hokkaido, but also whole landscape, like the heathlands landscapes, with heaths, small nomad trees, big dryad trees, scrubs and even bryophytes communities occurring together with the same dynamical relationships. Landscape of sloping forests with megaphorbs understorey are another example of this "landscape vicariance" phenomena.

VI. THE RUDERAL VEGETATION AND OTHERS

* Walking along the paths in Kushiro city, a European botanist is surprised by the similarities between European and Hokkaido's ruderal vegetation. In the surroundings of the harbour and of KIWC (Kushiro International Wetland Center), for example, one may see perennial herbaceous ruderal communities with *Geum aleppicum*, *Arctium lappa*, *Rumex obtusifolius*, *Artemisia vulgaris*, *Silene latifolia* subsp. *alba*, *Glechoma hederacea*, *Elytrigia repens*, *Rumex crispus*, *Melilotus officinalis*, *Oenothera parviflora*... very similar to the European communities, except the sporadic occurrence of *Petasites japonicus*, instead of *Petasites hybridus*, and the regular occurrence of a small white local geranium (*Geranium thunbergii*).

* The annual communities which may grow in mosaic with the former or the next one are characterized, as in Europe, by *Sisymbrium officinale*, *Sonchus oleraceus*, *Conyza canadensis*, *Senecio vulgaris*, *Stenactis annua*, *Chenopodium album*, *Thlaspi arvense*, *Poa annua*, *Matricaria discoidea*, *Stellaria media*, *Atriplex prostrata*, *Chenopodium glaucum*, *Rorippa palustris*...

* The trampled perennial vegetation is also dominated, like in Europe, by *Plantago major*, *Taraxacum* sect. *Ruderalia*, *Trifolium repens*, *Sagina procumbens*, *Agrostis capillaris*...

* On the shore emerged in summer (Lake Takobu for example), the annual eutrophilous community with *Bidens tripartita*, *Echinochloa crus-galli*... which has been observed should belong to the same class as in Europe (*Bidentetea tripartitae* Tüxen, Lohmeyer & Preising in Tüxen 1950).

* The maritime beach communities with *Honckenya peploides* var. *major*, *Leymus arenarius*, *Mertensia* sp. (*Mertensia maritima* ?) are vicariant of the one we may find in Northern Europe (as in Iceland for example) on sandy or gravelous substrate. But on the maritime cliffs, instead of finding grassland like in Europe, the Hokkaido's coasts exhibit megaphorbs (compare Ohba & Sugawara, 1979). This feature is very peculiar and may be perhaps correlated with a relative calm of the Pacific coastal waters, compare with the Atlantic one, so the salt spray could be rarer in Hokkaido. The tidal range seems to be smaller also, as may be recognised in the fact that brown Laminariales algae occur near the surface of the sea. At the border of the Hokkaido's cemetery for example, the steep slopes of the maritime cliff are occupied, even proximal to the sea, by a megaphorb community. The following relevé gives a good idea of its flora: (96/9/7, Ph. Julve, σ h: 100%, 0,60 m)

Sasa chartacea 4, *Adenophora trifoliata* 1, *Sanguisorba tenuifolia* 1, *Geranium yezoense* 1, *Dianthus superbus* var. *speciosus* 1, *Cirsium kamschaticum* 1, *Achillea ptarmica* var. *macrocephala* 1, *Rosa rugosa* juv. 1, *Calla palustris* 1, *Aster* sp. 1, *Ligularia hodgsonii* +, *Phalaris arundinacea* +, *Inula japonica* +, *Solidago virgaurea* +, *Galium verum* var. *trachycarpum* +, *Bupleurum longiradiatum* +, *Angelica edulis* +, *Carex* sp. +.

* The more exposed area are colonized by an open herbaceous community with *Ligusticum hulteni* and *Atriplex gmelinii*, replaced in the rockeries by a community with an unknown yellow flower plant accompanied by a local maritime form of *Daucus carota* s.l.

* At the upper subalpine belt of the mount Rausu and Chinshibetsu, we may observe an open scrub with *Betula ermanii*, *Alnus maximowiczii*, *Sorbus commixta*, *Acer tchonoskii*, *Pinus pumila*..., which may be a vicariant of the European *Alnus alnobetula* (= *A. viridis*) & *Betula alba* subsp. *glutinosa* (= *B. pubescens* subsp. *carpatica*) subalpine community of the Alps. This interesting community occurs in complex with a scattered tree community of *Abies sacchalinensis* & *Picea jezoensis* (*Picea jezoensis* - *Abies sacchalinensis* comm., with or without *Picea glehnii*), a megaphorb made of *Sasa kurilensis*, a hemisciaphilous forest herb-layer with *Cornus canadensis*, *Rhododendron aureum*, *Maianthemum dilatatum*, *Lycopodium annotinum*, *Vaccinium ovalifolium*, *Gaultheria miqueliana*, *Vaccinium axillare*, *Vaccinium vitis-idaea*, *Rubus pedatus*, *Eubotryoides grayana*, *Menziesia pentandra*, *Matteuccia struthiopteris*, *Phegopteris polypodioides*, *Gymnocarpium dryopteris*, *Shortia soldanelloides*... which has a strong relationship with the European herb-layer of coniferous boreo-subalpine forests.

* At the alpine belt, a community with *Arctostaphylos alpinus* var. *japonicus*, *Diapensia lapponica* var. *obovata*, *Empetrum nigrum* var. *asiaticum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Loiseleuria procumbens*, *Arctica nana* has been reported in bibliography (Numata, 1974). This flora is a vicariant of our European arctico-alpine *Loiseleuria procumbentis* - *Vaccinium uliginosi* subsp. *microphylli* Braun-Blanquet in Braun-Blanquet & Jenny 1926.

VII. CONCLUSIONS AND SOME GLOBAL THOUGHTS

What follows are, firstly, some conclusions inspired both by observations in the field and by the preceding analysis, and, secondly, a number of global thoughts about the structure of mire vegetation in general.

* At an holarctic level, at least, the mire bryophyte communities are largely the same, floristically and ecologically: they have the same role in the mire ecosystem and have the same edaphic and dynamic features (compare Miyawaki, 1968, Gimingham, 1984, Damman, 1988). In contrast, the vascular mire plant communities are less uniform at a world scale: other than under extreme conditions, these communities tend to show a geographical distribution reflecting both climate and chorological history and are less useful than bryophyte communities for describing edaphic conditions and dynamic stages. In this respect, many different ecological conditions, revealed by differing bryophyte communities, may be accompanied in a phytocoenotic complex by only a single vascular plant community. I regard this fact as one of the advantages of adopting a synusial approach to the functional description of mire vegetation.

* During the possible evolution of a mire, at a world scale (see Julve, 1996a for a formal structural explanation), we may observe a convergence of mire vegetation: the initial stages of fens may differ widely, whereas the terminal stages of bogs are largely similar. This fact may be demonstrated by the occurrence of different phytosociological classes (or subclasses) for the fens communities between Japan and Europe: *Moliniopsietea japonicae* versus *Scheuchzerio palustris* - *Caricetea nigrae*, or *Moliniopsienea japonicae* versus *Polygono vivipari* - *Caricenea nigrae* (Arctico-alpine), *Molinio caeruleae* - *Caricenea nigrae* (Middleeuropean), *Caricenea nigrae* subsp. *intricatae* (Altimediterranean) if we

Table 12.- Comparison of phytosociological mire units between Europe and Hokkaido.
 Tableau 12.- Comparaison des unités phytosociologiques des tourbières en Europe et à Hokkaido.

	EUROPE	HOKKAIDO
bog vascular vegetation		
ombrotrophic (towards mineralized heathland stage)	<i>Ledetalia palustris</i>	
	<i>Vaccinio microcarpi</i> - <i>Empetrium nigri</i> subsp. <i>hermaphrodit</i>	<i>Ledo palustris</i> subsp. <i>diversipilosi</i> - <i>Empetrium nigri</i> subsp. <i>japonici</i>
mineral soil water indicators limit (Mineralbodenwasserzeigergrenze)		
slightly minerotrophic	<i>Molinio caeruleae</i> – <i>Caricenea nigrae</i>	<i>Moliniopsienea japonicae</i>
	<i>Molinio caeruleae</i> subsp. <i>caeruleae</i> -	<i>Moliniopsio japonicae</i> -
pools	<i>Eriophorion vaginati</i> subsp. <i>vaginati</i>	<i>Eriophorion vaginati</i> subsp. <i>fauriei</i>
	<i>Drosero longifoliae</i> – <i>Rhynchosporotalia albae</i>	
	<i>Molinio caeruleae</i> subsp. <i>caeruleae</i> - <i>Rhynchosporion albae</i>	<i>Moliniopsio japonicae</i> - <i>Rhynchosporion albae</i>
floating mats	<i>Menyantho trifoliatae</i> - <i>Caricetalia lasiocarpae</i>	
fen vascular vegetation	<i>Molinio caeruleae</i> – <i>Caricenea nigrae</i>	<i>Moliniopsienea japonicae</i>
	<i>Polygono vivipari</i> – <i>Caricenea nigrae</i>	
	<i>Caricenea nigrae</i> subsp. <i>intricatae</i>	

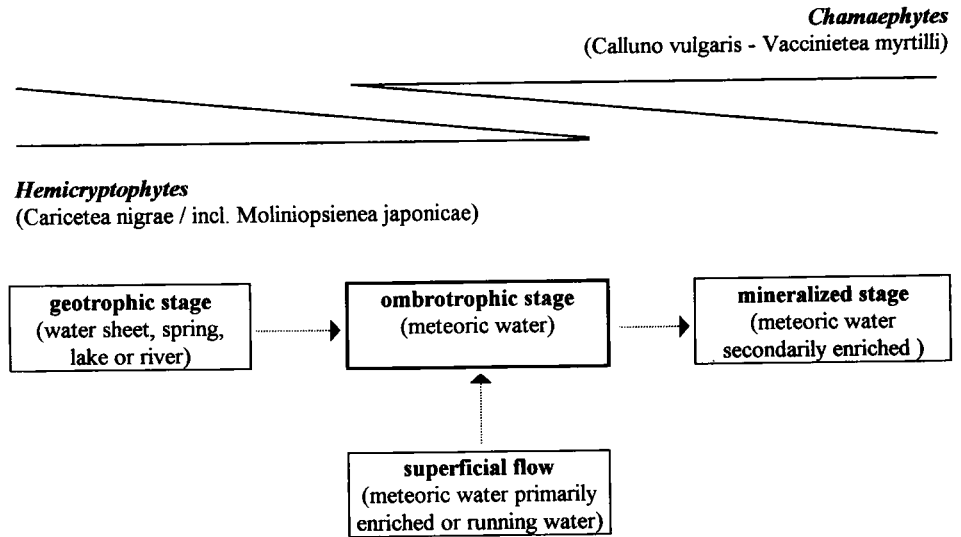
choose a subclass level). In contrast, the ombrotrophic bog vegetation in both regions belongs to the same order (*Ledetalia palustris*) which reflects the same ecological situations in both bogs vegetations. We must reach the alliance level to separate Japanese and European ombrotrophic bog vegetation, thus indicating the very close degree of similarity. In fact, during the primary succession stages, development of a mire shows an increasing independance from local ecological conditions : the mire builds its own medium. This explains the convergence of mire vegetation, at least in late dynamic stages, at a world scale (Table 12), beyond the mineral soil water indicators limit (*sensu* du Rietz 1954).

* Alongside the progressive succession observed in the development of mire vegetation (Julve, 1998c), we may see an increasing dominance of chamaephytes, accompanied by a decrease in the dominance and number of hemicryptophyte species. This phenomenon, whereby one biological type replaces another (Hemicryptophytes / Chamaephytes gradient in primary succession of mires), is remarkably constant at holarctic level, as is shown through the comparison between Hokkaido and Europe. These observations fit well within the concept of “ spectral sere ” as demonstrated by de Foucault (1995).

The hemicryptophytes mire's plants, which have their optimum in the fen classes, decrease along the possible succession of a mire, while chamaephytes, which have their optimum in heathland vegetation, increase with the possible succession. Some species of these classes (*Eriophorum vaginatum*, *Trichophorum cespitosum*, *Andromeda polifolia*, *Vaccinium oxycoccus*...) characterize the “ central ” mire communities, where they follow the concept of “ class end ” as defined by de Foucault (1981), but taken in a dynamical context and not in a chorological one (Table 13), see also de Foucault (1984). In fact we can talk about ecological limit instead of chorological limit, correlated with syntaxa impoverishment. Classically, the central vascular class of the ombrotrophic stage has been defined by the coexistence of chamaephytes (*Vaccinium oxycoccus*, *Andromeda polifolia*, *Ledum palustre*, *Betula nana*...) and hemicryptophytes (*Eriophorum vaginatum*, *Carex pauciflora*, *Drosera rotundifolia*, *Trichophorum cespitosum*...), but, following some ideas of Nordhagen (1936) and DuVigneaud (1949), these plants could be interpreted has the “ last plants ” of a “ class end phenomena ” (*sensu* de Foucault 1981, modified in ecological sense), and thus being considered as fen or heathland species, as new phytosociologi-

Table 13.- Generalized formal structure of the possible dynamic of a mire (after Julve, 1996a).

Tableau 13.- Structure formelle généralisée de la dynamique possible d'une tourbière (d'après Julve, 1996a).



cal synthesis suggests (see Julve, 1996a, b, 1998a, b, c, and works in progress, and Table 13.

* It is very interesting to note that, at least at holarctic level, only two types of leaf shape are to be found among mire plants :

- small rounded leaves, more or less applied horizontally on the substrate (e.g. *Parnassia palustris*, *Viola palustris*, *Viola epipsila*, *Anagallis tenella*, *Wahlenbergia hederacea*, *Drosera rotundifolia*, *Hydrocotyle vulgaris*, *Pinguicula vulgaris*, *Calla palustris*, *Rubus chamaemorus*, *Vaccinium oxycoccos*, *Vaccinium uliginosum*, *Chamaedaphne calyculata*, *Betula nana*...);
- thin and long erect or rarely patent leaves (e.g. all *Carex*, *Eriophorum*, *Rhynchospora*, *Trichophorum*, *Narthecium*, *Juncus*, *Calamagrostis*, *Equisetum*, *Andromeda polifolia*, *Drosera longifolia*, *Orchis laxiflora* subsp. *palustris*, *Dactylorhiza traunsteineri*, *Dactylorhiza maculata*, *Gymnadenia conopsea*, *Peucedanum lancifolium*, *Ledum palustre*, *Drosera intermedia*, *Galium boreale*, *Galium trifidum*...).

In plants, the vegetative shape is well suited to the prevailing environmental conditions, much more so than the generative shape, which are often more conservative. This essential conservatism of reproductive parts in plants is the reason why floristic classifications are based upon reproductive characters, and the adaptability of vegetative shape to environmental conditions follows faster evolution possibilities.

It is well known that some floristic families are significantly more represented in some habitats types (for example: *Rosaceae* in edges, *Chenopodiaceae* in eutrophic habitats, *Salicorniaceae* in salt marshes, *Asteraceae* in ruderal habitats, *Poaceae* in meadows, *Fabaceae* in grasslands, *Sarraceniaceae* and *Droseraceae* in mires...), but one can also see that some

families give one different representative species into each kind of habitat across a wide range of habitats (e.g. *Ranunculaceae*, *Apiaceae*, *Brassicaceae*, *Lamiaceae*, *Oenotheraceae*...). In this case, the representative species adopt, within the genetical constraint of its family, the shape fitted to the habitat. For mire plants, we can give some examples :

- for the “ thin erect ” shape, like the leaves of *Ranunculus flammula*, *Ranunculus lingua* (one is acidophilous the other neutrophilous, but both have markedly atypical leaf shapes for *Ranunculaceae* !), *Oenanthe lachenalii* (the finest leaves among *Apiaceae* !), *Carum verticillatum* (replacing the former in acidophilous habitats), *Scorzonera humilis* (an *Asteraceae* with fine leaves!), *Epilobium palustre* (the finest leaves in *Oenotheraceae*), *Euphorbia graminifolia* (well named), *Lobelia urens*, *Saxifraga hirculus* (thin leaves for a *Saxifragaceae* !), *Scutellaria minor* (thin leaves inside the *Lamiaceae*), *Veronica scutellata* (thin leaves for a *Scrophulariaceae* !);

- and for the “ small rounded ”, like the leaves of *Hydrocotyle vulgaris* (a rather strange leaf shape for an *Apiaceae* !), *Sanguisorba officinalis* (rounded shape of the leaflets of a compound leaf !), *Betula nana* (the roundest shape in the *Betulaceae*), *Calla palustris* (the most rounded of *Araceae*), *Liparis loeselii*, *Dactylorhiza fistulosa* (with patent leaves !), *Valeriana dioica* (the “ small roundest ” of the *Valerianaceae* !).

These shape features are represented equally both in Hokkaido and in European mires.

* de Foucault (1987) has shown that different kind of habitats may be characterised by systematic formal structures. He gives a formal way to describe these features, at the rank of families, and shows how useful they are for comparisons at world scale. The method involves doing “ relevés of families ” and subsequently working them into table in the manner of phytosociology. From this it is possible to recognise many systematic formal “ structures ” for mire vegetation: S(*Juncaceae*-*Cyperaceae*), S(*Lycopodiaceae*-*Ericaceae*), S(*Sphagnaceae*-*Ericaceae*), S(*Scheuchzeriaceae*-*Droseraceae*). As an example, the S(*Sphagnaceae*-*Ericaceae*) is sub-cosmopolitan, defined by the co-occurrence of *Ericaceae*, *Sphagnaceae* (both constant), *Droseraceae*, *Lycopodiaceae* (both less constant), *Empetraceae*, *Epacridaceae* (both geographically differential), accompanied by *Cyperaceae*, *Rosaceae*, *Liliaceae* and *Poaceae*. In this way it is possible to show that bog vegetation in Hokkaido and Europe adopts the same systematic formal structure at the family level in both places (another analysis could be carried out at the genus level).

* Many people have remarked that the initial stages of mires (whether naturally or perturbed dynamic) are characterised by green or brown sphagna (*Cuspidata* and *Subsecunda* groups), while terminal stages (more stable or climatic) are often dominated by red sphagna (*Acutifolia* group and *Sphagnum magellanicum*). I would simply mention that this mirrors what can be observed in marine environments, where red algae occupy stable environments while green and brown algae are found dominating more unstable localities (the medio-littoral zone, for example). The same is found with *Salicornia*, where the plants of lower tidal level (*Dolichostachya* group always flooded by the tide) become brownish or greenish in summer while the plants of upper tidal level (*Europaea* group, nearly never flooded, in stable environment) becomes reddish in summer. These “ European colour features.” may also be seen in Hokkaido, along the maritime coasts and in the mire.

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ANNEX

Syntaxonomic scheme of the seen Hokkaido's mire vegetation
(without trees and shrubs communities)

NB : see Julve (1998a, b) for the position and meaning of units present in Europe.

Phragmitis australis - *Caricetea elatae* Klika 1941

Order ? (corresponding to European *Phragmitetalia australis*)

Alliance ? (corresponding to European *Phragmiton australis*)

- *Zizania latifoliae* - *Schoenoplectetum lacustris* ass. nov.

Order ? (corresponding to European *Caricetalia elatae*)

Alliance ? (corresponding to European *Caricion rostratae*)

- *Thelypterido nipponicae* - *Phragmitetum australis* ass. nov.

- community with *Calamagrostis langsdorffii*

Scheuchzeria palustris - *Caricetea nigrae* subsp. *nigrae* (Nordhagen 1936) Tüxen 1937 *em.*

Moliniopsiensea japonicae (Suzuki & Arakane 1970) subclass. nov.

Order ? (corresponding to Middle-european *Junco acutiflori* - *Caricetalia nigrae*)

Moliniopsis japonicae - *Eriophorion vaginati* subsp. *fauriei* all. nov.

- *Carici oligospermae* - *Eriophoretum vaginati* ass. nov.

(= *Moliniopsis japonicae* - *Eriophoretum vaginati* apud Suzuki 1975 p.p. ?)

- *Geo pentapetali* - *Caricetum middendorffii* ass. nov.

(incl. *Geum pentapetalum* - *Carex middendorffii* comm. apud Suzuki 1975)

(incl. *Carici middendorffii* - *Vaccinium oxycocci* apud Suzuki 1975 ?)

Potentilla palustris - *Menyanthes trifoliatae* Julve 1998

Menyantho trifoliatae - *Caricetalia lasiocarpae* Julve 1993

Alliance ?

- *Eriophoro gracilis* subsp. *coreanum* - *Caricetum lasiocarpae*

subsp. *occultans* ass. nov.

(= *Myrica gale* var. *tomentosa* - *Carex lasiocarpa* subsp. *occultans* comm.)

- community with *Carex lyngbyei* & *Carex rhynchohypsa*

(*Caricetum rhynchohypsa* apud Suzuki 1975 ?)

- community with *Lysichiton camtschatcense*

Drosero longifoliae - *Rhynchosporietalia albae* Tüxen 1980

Moliniopsis japonicae - *Rhynchosporion albae* Tüxen, Suzuki & Fujiwara 1970

- *Rhynchosporo fauriei* - *Caricetum limosae* Miyawaki & Fujiwara 1970

(= *Scheuchzeria palustris* - *Rhynchosporietum albae* apud Suzuki 1975 ?)

Eriocaulo sikokiani - *Rhynchosporion fujianae* Fujiwara 1979

- *Utriculario yakusimensis* - *Eriocaulum sikokiani* Fujiwara 1979

Calluna vulgaris - *Vaccinieta myrtilli* (Braun-Blanquet, Sissingh & Vlieger 1939) de Foucault 1990

Ledetalia palustris Nordhagen 1936

Ledo palustris subsp. *diversipilosi* - *Empetrium nigri*

subsp. *japonici* (Tüxen, Miyawaki & Fujiwara 1972) all. nov.

- *Rhododendro parvifolii* - *Chamaedaphnetum calyculatae* ass. nov.

- *Coptido trifoliae* - *Caricetum pauciflorae* ass. nov.

Aulacomnion palustris - *Sphagnetalia fallacis* Julve 1992 *ex hoc loco*

Aulacomnion palustris - *Sphagnetalia fallacis* Julve 1992 *ex hoc loco*

Sphagnion rubello - *magellanici* Gillet prov. in Julve 1992 *ex hoc loco*

- *Mylio anomalae* - *Sphagnetum fusci* (Cajander 1913) Julve 1993 *ex hoc loco*

- *Sphagnetum rubello* - *magellanici* (Osvald 1923) Julve 1996 prov.

- community with *Sphagnum imbricatum* & *Sphagnum subfulvum*
Warnstorffia exannulata (Krajina 1933) Julve 1996
- community with *Sphagnum papillosum*
- community with *Sphagnum russowii*
- Sphagnion cuspidati* Chipon, Deny, Estrade, Nardin & Vadam 1988
 - *Cladopodiella fluitantis* - *Sphagnetum cuspidati* (Osvold 1923) Julve 1996 prov.