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Title	Ecological Gradients of North Japanese Mires on the Basis of Hydrochemical Features and Nitrogen Use Traits of Carex Species
Author(s)	Nakamura, Takatoshi
Citation	Eurasian Journal of Forest Research, 6(2), 117-130
Issue Date	2003-09
Doc URL	<a href="https://hdl.handle.net/2115/22167">https://hdl.handle.net/2115/22167</a>
Type	departmental bulletin paper
File Information	6(2)_P117-130.pdf



## Ecological Gradients of North Japanese Mires on the Basis of Hydrochemical Features and Nitrogen Use Traits of *Carex* Species

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### Abstract

Habitat preferences and N use traits of six *Carex* species characterizing the floristic variation in mire ecosystems were examined in seven lowland mires throughout Hokkaido, northern Japan. Canonical Discriminant Analysis showed that soil water pH was the strongest discriminant between habitats of the *Carex* species, with total dissolved nitrogen (TDN) concentration also contributing, independently of pH. Two major patterns were apparent in the distribution of *Carex* species along pH and TDN concentration: pH determines a bimodal distribution into fens with pH > 5.0 and bogs with pH < 5.5, whilst TDN captures the variation in productivity within both fen and bog, but does not differ significantly between them. Although N use efficiency (NUE) and mean residence time of N in plant tissues (MRT) of the sedge plants growing in the weakly acidic habitats (fens) correlated negatively with TDN, they were constantly high in the acidic habitats (bogs) regardless of the TDN concentration. Responses of N productivity (*A*) did not correlate with TDN in either fens or bogs. Accordingly, the trade-off between *A* and MRT along habitat N richness theoretically predicted does not necessarily apply to wetland vegetation, because the ecological performances of the *Carex* species would be dominated by the soil water acidity rather than the N richness. The relationship between N use traits and habitat preferences along pH and N richness of the *Carex* species derived the ecological rationales of the vegetation pattern through the ecophysiological performance of individual species. These results would much contribute to essential knowledge and practical information for the conservation and restoration of north Japanese lowland mires facing to the serious crisis by direct and indirect impacts.

*Key words:* mire vegetation, nitrogen richness, nitrogen-use strategy, pH, productivity

### Introduction

#### Function and importance of mires

Mires distributing broadly in the boreal and cool temperate climate areas of the Northern Hemisphere have been recognized as one of the important terrestrial carbon sinks along with tropical rain forests and tropical wetland forests (Franzén *et al.* 1996, Ohlson and Økland 1998). However, function as carbon sink in mires, which accumulates large amount of organic carbon in the peat soil, can be possibly exchanged to carbon source to atmosphere with acceleration in the peat decomposing rate due to the recent global warming and/or artificial disturbances. Whereas, mire ecosystems including the surrounding area in a wide sense play multilateral roles for conservation of natural resources, e.g. maintaining of biodiversity, retention of water resource, and buffer zone to intense change in hydrochemical environments (Verhoven 1992).

According to the drastic expansion of human activity areas such as urbanization or large-scale development of pastureland since early 20th century, mire area has been greatly reduced in various places (e.g. Carter 1986, Vermeer and Joosten 1992, Yabe 1993). In addition to the conspicuous reduction at landscape level, the remained mires are critically threatened in its quality through eutrophication, dehydrate, enrichment of mineral elements and fragmentation of the ecosystems

(e.g. Ehrenfeld and Schneider 1991, De Mars *et al.* 1996, Yabe *et al.* 2001). In northern Europe and North America, serious acidification and nitrogen deposition due to an atmospheric pollution have been widely occurred in the mire ecosystems as well as in the forest ecosystems, and studies on the effects of air pollution and on the restoration of damaged and lost mires by intense exploitations have been actively carried out (e.g. Ehrenfeld and Schneider 1991, Ferland and Rochefort 1997, Beltman *et al.* 1996, Verhoeven *et al.* 1996, Budelsky and Galatowitsch 2000, Gunnarsson *et al.* 2000).

In Hokkaido, northern Japan, wide area of lowland mires has already disappeared during 20th century (Yabe 1997), and most remaining mires are critically facing to the serious damage by artificial disturbance. For instance, inflow of base cations from the surrounding urban areas or adjacent road threatens well developed *Sphagnum* communities in the Kiushito mire and the Utsai mire (Yabe *et al.* 1999, Yabe *et al.* 2001), and excess N availability by horse pasturage in the Tohfutsu mire contributes to an anomalous distribution pattern in the vegetation, i.e. occurrence of less productive communities in the most fertile habitats (Nakamura *et al.* 2002). Except for the assessment of economical values for agricultural production, however, ecological studies relating to hydrochemical features of

mires have been scarcely conducted in Japan, probably because the significance of mires has not been substantially recognized as important natural resources. It is an urgent necessity to accumulate the fundamental information from various aspects of the nature for the conservation of the remained mires and for the restoration of the damaged mires.

#### **Carex species as useful indicators of mire environments**

*Carex* species are commonly dominating in various types of mire vegetation in the Northern Hemisphere and characterize the floristic variation, vegetation structure, community productivity, and hydrochemistry of habitats (e.g. Ellenberg 1988, Budelsky and Galatowitsch 2000). Thus, they will provide excellent knowledge and information for environmental and ecophysiological approaches to global comparison both on the vegetation pattern and on the plant performance. Moreover, quantitative analyses of *Carex* species at community level and at individual level are expected to reveal the vegetation responses to possible alteration of hydrochemical environments in the future.

The present study focuses on the two ecological aspects of mire ecosystems: first, relationship between mire vegetation and hydrochemical environments based on habitat preferences of *Carex* species, and second, function of ecophysiological performance of individual *Carex* species in the vegetation pattern.

#### **Hydrochemical approach**

Floristic variation in mire ecosystems in cool and moist climates is strongly correlated with the origin and chemistry of the water that passes through them (Ellenberg 1988, Richardson 1988). Interaction between the water supply and the rate of decomposition of organic debris influences floristic variation along the hydrochemical gradient as a result of variations in water level, acidity and nutrient status (Malmer 1986). Of fens with a minerotrophic water supply, rich fen is typically dominated by dicotyledonous herbs and grasses with some characteristic calcicole plants (Kooijman and Westhoff 1995), whereas poor fen is usually dominated by sphagna with calcifuge Cyperaceae and dwarf *Carex* and *Juncus* species (Du Rietz 1949). pH and concentration of base cations in rich fens are generally higher than in poor fen or bog dominated by sphagna and dwarf ericaceous shrubs (Waughman 1980, Vitt and Chee 1990, Wells 1996).

Nutrient richness is also the factor distinguishing between the hydrochemical properties of fen and bog (Ellenberg 1988), and is closely linked with floristic variation and productivity of vegetation in mires (Verhoeven *et al.* 1983, Kooijman and Westhoff 1995). The relation between nutrient richness and vegetation is not simple, however. In NW European mires the difference in plant nutrient availability between fens and bogs remains unclear (Waughman 1980, Verhoeven *et al.* 1988, Verhoeven *et al.* 1990). In west Canadian mires, the occurrence of fen or bog is related to acidity-alkalinity rather than nutrient status (Vitt *et al.* 1995). Furthermore, eutrophication and acidification as

a result of recent atmospheric pollution has made the relation between floristic variation and environment difficult to study. In their review of gradient relations in NW European mires, Wheeler and Proctor (2000) demonstrated that the distinction between fen and bog (including poor fen) is reflected in a bimodal distribution of pH. They also found that some floristic variation within both fen and bog is explained by the availability of limiting nutrients such as N and P.

The relation between floristic variation and hydrochemistry in NE Asian mires has not been closely studied. In Hokkaido, northern Japan, where there are no lime-rich mires (Wolejko and Ito 1986), floristic variation arises mostly as a result of periodic flooding due to the monsoon climate (Yabe and Onimaru 1997, Hotes *et al.* 2001). These observations suggest that the hydrochemical properties of fen and bog, in particular, their acidity, base richness and nutrient status, should be studied comprehensively.

#### **Ecophysiological approach**

Most of previous studies in mire ecosystem have confined within correlative comprehension between plant distribution and environmental variables. On the other hand, physiological studies on nutrient use strategy of plants have attempted ecologically to explain the plant distribution and mechanisms in natural fields.

In general, nitrogen (N) availability is closely associated with plant productivity (Vermeer and Berendse 1983, Wheeler 1983), and often limits plant N uptake in terrestrial ecosystems (e.g. Tilman 1985, Vitousek and Howarth 1991). Wild plants must compete to obtain the limited N that is available, retain the N that they absorb, or both. Advantage in competition for N depends on traits that maximise N capture and N assimilation (Tilman 1988). N retention in plants depends on traits that minimize N loss (Chapin 1980).

These traits may, to some extent, be mutually exclusive: competitive plants would be unlikely to be as successful in retaining N. Berendse and Aerts (1987) formalised this trade-off. They emphasized the need to examine two components of plant N use efficiency (NUE); that is, N productivity ( $A$ : the rate of biomass increase per unit of N in the plant) and mean residence time of N in a plant (MRT). In N-rich habitats, increasing the rate of dry-matter production (i.e. increasing  $A$ ) should be more adaptive, whereas reducing nutrient loss and maximising nutrient resorption (prolonging MRT) would be more adaptive in nutrient-poor habitats (Berendse and Aerts 1987). Therefore, there should be a trade-off between  $A$  and MRT along gradients of N availability.

The NUE of many different species has been studied in relation to habitat fertility. For instance, the NUE of evergreen species, which tend to dominate nutrient-poor habitats, exceeds the NUE of deciduous species that usually dominate nutrient-rich habitats (Vitousek 1982, Chapin and Shaver 1989). In Dutch heathlands, Aerts (1990) found a trade-off between  $A$  and MRT in evergreen shrubs with smaller  $A$  and longer

MRT and in deciduous grasses with larger  $A$  and shorter MRT. The predicted trade-off between  $A$  and MRT was found in two Swedish wetlands even though variations in neither  $A$  nor MRT were related to habitat fertility (Eckstein and Karlsson 1997). Variations in  $A$  and MRT among plants with the same life form do not always support the theory (e.g. Aerts and De Caluwe 1994, Vazquez de Aldana and Berendse 1997), but these studies were not done under field conditions. It has not been generally known if the trade-off between  $A$  and MRT exists among plants growing in their natural habitats and, if it does, if it is related to habitat fertility.

Possible reasons for the above uncertainty include the following:

1. Effects of phylogenetic differences have not been considered (Kasuya 1995).
2. No field studies on the relationship between intraspecific variation and interspecific differences in  $A$  and MRT have yet been reported.
3. NUE traits have been examined mostly by comparisons among habitats within environmental ranges narrower than the whole range that the habitats occupy.
4. The range of ecosystems studied has not truly reflected nutrient availability *per se*. For example, bogs or heaths have usually been assumed to be primarily nutrient-poor habitats, although each is more strongly characterized by their low pH (Wheeler and Proctor 2000). In west European mires, the combined effects of acidification and eutrophication from atmospheric pollution have accelerated the succession from species-rich fens to species-poor bogs (Beltman *et al.* 1996, Gunnarsson *et al.* 2000). In such ecosystems, plant nutrient use may not be correlated strongly with nutrient availability, but instead reflect the influence of habitat pH on nutrient use traits.

The ecophysiological approach is undeniably expected to make clear the plant distribution mechanisms in mire ecosystem through the test on the existence of hypothesised trade-off between  $A$  and MRT.

The aims of this study are (i) to simplify the general relationship between variations in mire vegetation and hydrochemical variables on the basis of distribution patterns of the *Carex* species commonly growing in the north Japanese mires, and (ii) to provide fundamental knowledge for the conservation and restoration of mire ecosystems through the ecophysiological apprehensions with special reference to N use traits of the *Carex* plants.

## Materials and Methods

### Sites and plants studied

Seven relatively little-damaged lowland mires were chosen throughout Hokkaido, i.e. Asajino, Sarobetsu, Tohfutsu, Fuhrengawa, Oikamanai (including the adjacent area), Yufutsu and Utasai (Fig. 1). These mires consist of differing scales of fragments of bog supplied with ombrotrophic or weakly minerotrophic water, and

of fen supplied with obviously minerotrophic water for at least one period each year. In the field, bog and fen were classified by presence or absence of *Sphagnum* cover in addition to the coexistence of specific bog species such as *Chamaedaphne calyculata* (L.) Moench, *Vaccinium microcarpum* (Turcz.) Schmalh., etc. The annual mean temperature and the mean annual precipitation observed at meteorological stations near each mire vary from 5°C to 7°C and from 730 mm to 1430 mm.

The following six *Carex* species that are common in lowland mires of NE Asia were studied: *C. limosa* L., *C. middendorffii* Fr. Schm., *C. lasiocarpa* Ehrh. var. *occultans* (Franch.) Kükenth., *C. pseudocuraica* Fr. Schm., *C. thunbergii* Steud. var. *appendiculata* (Trautv.) Ohwi, and *C. lyngbyei* Hornem. (Table 1). Within the seven mires, a total of 270 sampling sites was set in stable communities dominated by one of these sedges. All the data set were used for the examination of distribution pattern of these species, but all the sites in stoloniferous *C. pseudocuraica*, two in *C. middendorffii*, one in *C. lasiocarpa*, and one in *C. lyngbyei* were precluded from the analyses for the examination of N use traits to avoid the effects of difference in life form and physical disturbance by herbivorous insects within a year.

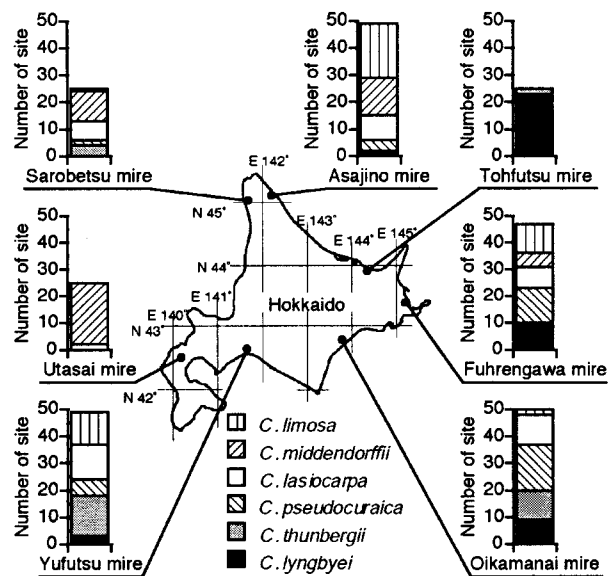


Fig. 1. Location of the mires investigated and the number of sample for each *Carex* species.

### Hydrochemistry environments of habitats

In each of the 270 sites a plastic pipe, 50 cm long and 3 cm in diameter, in which many holes (5 mm in diameter) had been bored, was driven into the soil, so as to measure the water level from the ground surface. Measurements were conducted in late July and early November 1998. The water level of each site was defined as the mean value of the two measurements.

Table 1. Characteristics of the six *Carex* species studied and number of sites sampled

Species	Size/Habit	Occurrence	Associated species	Number of sites
<i>C. limosa</i>	Small, slender	Weakly minerotrophic fens and bogs	<i>Rhynchospora alba</i> (L.) Vahl, <i>Scheuchzeria palustris</i> L., <i>Eriophorum gracile</i> Koch., <i>Utricularia intermedia</i> Hayne, <i>Menyanthes trifoliata</i> L., <i>Sphagnum papillosum</i> Lindb.	46
<i>C. middendorffii</i>	Small to middle, stout, sporadically tussocked	Bogs	<i>Eriophorum vaginatum</i> L., <i>Vaccinium microcarpum</i> (Turcz.) Schmalh., <i>Hemerocallis middendorffii</i> Trautv. et May., <i>Hosta recutifolia</i> Nakai, <i>Moliniopsis japonica</i> (Hack.) Hayata, <i>Sphagnum papillosum</i> , <i>Sphagnum palustre</i> L.	53
<i>C. lasiocarpa</i> var. <i>occultans</i>	Middle, slender, somewhat firm	Weakly minerotrophic fens and sporadically in bogs	<i>Phragmites australis</i> W. Clayton, <i>Alnus japonica</i> Steud., <i>Lobelia sessilifolia</i> Lamb., <i>Sphagnum recurvum</i> P. Beauv.	50
<i>C. pseudocuraica</i>	Middle, stoloniferous	Flooded depressions of minerotrophic fens in flood plains	<i>Phragmites australis</i> , <i>Calamagrostis langsdorffii</i> (Link) Trin., <i>Equisetum limosum</i> L., <i>Lastrea thelypteris</i> (L.) Bory	42
<i>C. thunbergii</i> var. <i>appendiculata</i>	Middle to large, densely packed	Minerotrophic fens	<i>Lycopus uniflorus</i> Michx., <i>Phragmites australis</i> , <i>Juncus wallichianus</i> Laharpe	32
<i>C. lyngbyei</i>	Very large, stout, forming a large mat	Minerotrophic fens	<i>Phragmites australis</i> , <i>Rubia jesoensis</i> (Miq.) Miyabe et Miyake, <i>Lysimachia thyrsiflora</i> L., <i>Cicuta virosa</i> L.	47

To examine the soil water chemistry at each site, another closed-bottom plastic pipe, 30 cm long and 3 cm in diameter in which many holes (3 mm in diameter) had been bored in the central section, was temporarily inserted. This allowed collection of the soil water at depth 10 to 20 cm from the soil surface, where most of the root systems are concentrated. After driving the pipe into the soil, its interior was depressurized using a portable vacuum pump, and was collected the seepage soil water in the pipe.

Electrical conductivity (EC) and pH were measured *in situ* using a portable EC meter (CM-14P, TOA, Tokyo) and a pH meter (HM-12P, TOA, Tokyo), respectively, and then about 250 ml of the sampled water was stored in a polyethylene bottle. The conductivity of H<sup>+</sup> ions was subtracted from the sample conductivity values (Sjörs 1952). In the laboratory the samples were filtered through a 0.45 µm membrane filter, and the nutrient concentrations were then determined as follows (Japan Society for Analytical Chemistry, Hokkaido Branch 1994): total dissolved nitrogen (TDN) by the alkaline potassium peroxodisulphate-ultraviolet spectrophotometric method; ammonium-nitrogen (NH<sub>4</sub>-N) by the indophenol blue method; total dissolved phosphorus (TDP) by the potassium peroxodisulfate-molybdate blue method; and phosphate-phosphorus (PO<sub>4</sub>-P) by the molybdate blue method. Concentrations of minerals

such as Na, Ca, K, Mg and Fe were examined by atomic absorption spectroscopy (AA-625-11, Shimadzu, Kyoto).

In each site, sampling was performed in early November 1998. Because the change in soil water chemistry caused by plant nutrient absorption was expected to be minimal in late autumn, values should indicate accurately the potential nutrient availability for plants.

#### Aboveground biomass and plant nitrogen content

In July 1998, when the biomass of living plant parts was the maximum, the aboveground vegetation was mowed on a 0.5 x 0.5 m quadrat within each the 270 sites for the analyses of distribution patterns. All non-*Carex* species were removed from the samples harvested. After drying for at least 48 h at 70 °C in an oven, the total dry mass of each quadrat was measured. The dry mass data were calculated as aboveground biomass per unit area. Shoot sampling of the *Carex* species were conducted in July and November 1998 in each the 224 sites for the analysis of N use traits. In July, ten non-reproductive living shoots were randomly sampled in each site, and the total dry mass of each shoot sample was measured after drying as above. In November, when the aboveground parts of the *Carex* species were dead, ten dead shoots were randomly sampled and measured their dry mass, as July sample.

These shoot data were used to estimate the dead *Carex* biomass per unit area in November, which the area-based biomass in November were calculated by products of the shoot-based biomass in November and ratio of the area-based biomass in July and the shoot-based biomass in July.

All shoot samples were milled, and their total N concentrations were analyzed using a C/N analyzer (NC/900, Shimadzu, Kyoto). Total N contents of the green shoots per unit area ( $\text{g N m}^{-2}$ ) in July were calculated from N concentrations ( $\text{g N g DM}^{-1}$ ) and area-based biomass ( $\text{g DM m}^{-2}$ ) in July; those of the dead plants were calculated from the equivalent of the November data.

### Discrimination of habitats

The multivariate technique Canonical Discriminant Analysis (CDA) was used to detect differences in hydrochemical environments among *Carex* species. CDA is usually used to discriminate between more than three groups with multivariate factors; it finds linear combinations of discriminating variables, which maximize the difference between groups, and allows for interaction between factors. In running CDA, ineffective factors were progressively eliminated (Step-wise forward method:  $F\text{-in} > 3.5$ ,  $p < 0.001$ ). All statistical analyses were run using STATISTICA 5.1 for Windows (StatSoft 1997).

### Parameters in nitrogen use trait

For the parameters of N use trait, NUE ( $\text{g DM g N}^{-1}$ ),  $A$  ( $\text{g DM g N}^{-1} \text{ yr}^{-1}$ ) and MRT (yr) were calculated as follows:

$$\text{NUE} = \text{NPP} / \text{N}_{\text{LOSS}} \quad \text{eqn 1}$$

$$A = \text{NPP} / \text{N}_{\text{POOL}} \quad \text{eqn 2}$$

$$\text{MRT} = \text{N}_{\text{POOL}} / \text{N}_{\text{LOSS}} \quad \text{eqn 3}$$

where NPP ( $\text{g DM m}^{-2} \text{ yr}^{-1}$ ),  $\text{N}_{\text{LOSS}}$  ( $\text{g N m}^{-2} \text{ yr}^{-1}$ ) and  $\text{N}_{\text{POOL}}$  ( $\text{g N m}^{-2}$ ) are net primary productivity, N loss in autumn, and average N content in a growing season, respectively (see Appendix). The aboveground biomass of dead plants per unit area in November was used for NPP, because the populations would be stable and the amounts of carbon and N translocated from roots to shoots in spring would have equilibrated with those reallocated from shoots to roots in autumn. Because the aboveground parts of these species barely survive

through November, it was assumed that  $\text{N}_{\text{LOSS}}$  was equal to the N content in dead shoots per unit area in November, and  $\text{N}_{\text{POOL}}$  was equivalent to half of the N content in green shoots per unit area in July. NUE is the reciprocal of N concentration in dead plants and is equal to the product of  $A$  and MRT.

## Results

### Aboveground biomass

The aboveground biomass was largest for *C. lyngbyei*, a typical fen species and moderate for *C. thunbergii*, another fen species, and for *C. pseudocuraica* and *C. lasiocarpa*, which are common in weakly minerotrophic fens. *C. middendorffii*, a typical bog species, had lower values and *C. limosa*, which grows in fens and bogs, the least (Table 2). Aboveground biomass was strongly related to the origin of the water supply: larger species predominated in minerotrophic sites, and smaller ones in ombrotrophic to weakly minerotrophic sites. Aboveground biomass per shoot showed similar trends with those per unit area except for stoloniferous *C. pseudocuraica*.

### Hydrochemical environments of habitats

Interspecific differences were statistically significant for all the environmental variables measured (Table 3). WL and pH were lowest for the bog species *C. middendorffii*, and were higher for the productive fen species *C. thunbergii* and *C. lyngbyei* than for the other species. Higher TDN concentrations were observed for *C. thunbergii* and *C. lyngbyei*, but higher TDP concentration only for *C. lyngbyei*. Electrical conductivity and  $\text{NH}_4\text{-N}$  concentration were higher for *C. thunbergii* than for the other species. The concentrations of  $\text{PO}_4\text{-P}$ , Mg, Na and K showed similar trends in being highest for the most productive species, *C. lyngbyei*. The Fe concentration was lowest for *C. pseudocuraica*. Of the base minerals, the mean concentrations for Ca and Mg were very low for all species, at 1.17-2.60 and 0.95-1.81  $\text{mg L}^{-1}$ , respectively. A relatively high concentration of Na was found for every species, indicating a maritime influence on the water chemistry of the lowland mires in this study.

Table 2. Mean ( $\pm$  SE) aboveground biomass per unit area and per shoot of the six *Carex* species. Means in the same row followed by the same letter do not differ significantly according to Scheffe's multiple-comparison test ( $p < 0.05$ ). For *C. pseudocuraica* only the biomass per unit area is shown, since its stoloniferous form makes shoots impossible to distinguish.

	<i>C. limosa</i> ( $n = 46$ )	<i>C. middendorffii</i> ( $n = 53$ )	<i>C. lasiocarpa</i> ( $n = 50$ )	<i>C. pseudocuraica</i> ( $n = 42$ )	<i>C. thunbergii</i> ( $n = 32$ )	<i>C. lyngbyei</i> ( $n = 47$ )
Biomass / area ( $\text{g DM m}^{-2}$ )	87 $\pm$ 6.8 <sup>a</sup>	151 $\pm$ 8.4 <sup>ab</sup>	203 $\pm$ 16.2 <sup>bc</sup>	255 $\pm$ 16.3 <sup>c</sup>	289 $\pm$ 24.9 <sup>c</sup>	520 $\pm$ 40.0 <sup>d</sup>
Biomass / shoot ( $\text{g DM shoot}^{-1}$ )	0.14 $\pm$ 0.01 <sup>a</sup>	0.32 $\pm$ 0.01 <sup>ab</sup>	0.47 $\pm$ 0.03 <sup>b</sup>	-	0.46 $\pm$ 0.03 <sup>b</sup>	2.50 $\pm$ 0.13 <sup>c</sup>

Table 3. Hydrochemical environments (mean  $\pm$  SE) of the habitats of the six *Carex* species. *F*-values are obtained by ANOVA in each variable ( $p < 0.05$  for all the variables). Means in the same row followed by the same letter do not differ significantly according to Scheffe's multiple-comparison test ( $p < 0.05$ ).

Environmental variable	<i>C. limosa</i> ( <i>n</i> = 46)	<i>C. middendorffii</i> ( <i>n</i> = 53)	<i>C. lasiocarpa</i> ( <i>n</i> = 50)	<i>C. pseudocuraica</i> ( <i>n</i> = 42)	<i>C. thunbergii</i> ( <i>n</i> = 32)	<i>C. lyngbyei</i> ( <i>n</i> = 47)	<i>F</i> -value
WL (cm)	3.9 $\pm$ 0.77 <sup>c</sup>	-5.7 $\pm$ 0.62 <sup>a</sup>	1.7 $\pm$ 0.88 <sup>b</sup>	4.4 $\pm$ 0.60 <sup>c</sup>	6.0 $\pm$ 0.90 <sup>c</sup>	6.2 $\pm$ 0.70 <sup>c</sup>	38.18
pH	5.49 $\pm$ 0.12 <sup>b</sup>	4.54 $\pm$ 0.06 <sup>a</sup>	5.60 $\pm$ 0.11 <sup>b</sup>	5.66 $\pm$ 0.09 <sup>b</sup>	6.25 $\pm$ 0.11 <sup>c</sup>	5.74 $\pm$ 0.07 <sup>b</sup>	35.97
TDP (mg L <sup>-1</sup> )	0.060 $\pm$ 0.009 <sup>a</sup>	0.074 $\pm$ 0.004 <sup>a</sup>	0.047 $\pm$ 0.010 <sup>a</sup>	0.026 $\pm$ 0.005 <sup>a</sup>	0.040 $\pm$ 0.008 <sup>a</sup>	0.140 $\pm$ 0.022 <sup>b</sup>	12.07
TDN (mg L <sup>-1</sup> )	0.48 $\pm$ 0.05 <sup>ab</sup>	0.68 $\pm$ 0.03 <sup>bcd</sup>	0.56 $\pm$ 0.05 <sup>ac</sup>	0.40 $\pm$ 0.05 <sup>a</sup>	0.84 $\pm$ 0.09 <sup>cd</sup>	0.90 $\pm$ 0.07 <sup>d</sup>	11.81
EC (mS m <sup>-1</sup> )	9.55 $\pm$ 1.19 <sup>a</sup>	6.51 $\pm$ 0.54 <sup>a</sup>	8.71 $\pm$ 0.67 <sup>a</sup>	7.75 $\pm$ 0.66 <sup>a</sup>	17.82 $\pm$ 2.69 <sup>b</sup>	10.84 $\pm$ 0.47 <sup>a</sup>	11.68
PO <sub>4</sub> -P (mg L <sup>-1</sup> )	0.037 $\pm$ 0.007 <sup>a</sup>	0.049 $\pm$ 0.003 <sup>a</sup>	0.029 $\pm$ 0.008 <sup>a</sup>	0.011 $\pm$ 0.002 <sup>a</sup>	0.019 $\pm$ 0.005 <sup>a</sup>	0.083 $\pm$ 0.015 <sup>b</sup>	9.79
Mg (mg L <sup>-1</sup> )	0.95 $\pm$ 0.05 <sup>a</sup>	1.23 $\pm$ 0.09 <sup>a</sup>	1.06 $\pm$ 0.08 <sup>a</sup>	1.01 $\pm$ 0.10 <sup>a</sup>	1.15 $\pm$ 0.18 <sup>a</sup>	1.81 $\pm$ 0.16 <sup>b</sup>	7.82
NH <sub>4</sub> -N (mg L <sup>-1</sup> )	0.086 $\pm$ 0.026 <sup>ab</sup>	0.019 $\pm$ 0.004 <sup>a</sup>	0.034 $\pm$ 0.005 <sup>a</sup>	0.017 $\pm$ 0.004 <sup>a</sup>	0.165 $\pm$ 0.054 <sup>b</sup>	0.046 $\pm$ 0.006 <sup>a</sup>	6.90
K (mg L <sup>-1</sup> )	0.78 $\pm$ 0.10 <sup>a</sup>	0.75 $\pm$ 0.18 <sup>a</sup>	0.78 $\pm$ 0.10 <sup>a</sup>	1.11 $\pm$ 0.12 <sup>ab</sup>	0.95 $\pm$ 0.10 <sup>a</sup>	1.85 $\pm$ 0.29 <sup>b</sup>	6.33
Ca (mg L <sup>-1</sup> )	1.71 $\pm$ 0.21 <sup>ab</sup>	1.17 $\pm$ 0.05 <sup>a</sup>	1.63 $\pm$ 0.11 <sup>ab</sup>	1.91 $\pm$ 0.23 <sup>ab</sup>	2.60 $\pm$ 0.40 <sup>b</sup>	2.14 $\pm$ 0.17 <sup>b</sup>	6.04
Fe (mg L <sup>-1</sup> )	0.25 $\pm$ 0.06 <sup>ab</sup>	0.38 $\pm$ 0.03 <sup>b</sup>	0.27 $\pm$ 0.04 <sup>ab</sup>	0.13 $\pm$ 0.03 <sup>a</sup>	0.45 $\pm$ 0.12 <sup>b</sup>	0.25 $\pm$ 0.03 <sup>ab</sup>	4.19
Na (mg L <sup>-1</sup> )	6.62 $\pm$ 0.38 <sup>a</sup>	7.23 $\pm$ 0.69 <sup>ab</sup>	6.96 $\pm$ 0.54 <sup>a</sup>	6.84 $\pm$ 0.92 <sup>ab</sup>	10.93 $\pm$ 3.76 <sup>ab</sup>	12.89 $\pm$ 1.01 <sup>b</sup>	4.17

Table 4. Standardized coefficients of environmental variables in each canonical discriminant function (*n* = 270).

	Canonical function			
	1	2	3	4
WL	0.51	-0.45	0.66	-0.37
pH	0.68	0.23	-0.56	0.44
TDN	0.36	1.44	-0.78	0.95
NH <sub>4</sub> -N	-0.03	-0.51	-0.28	-0.87
TDP	0.25	0.01	0.70	-0.88
Fe	-0.22	-0.93	0.04	-1.09
Eigenvalue	1.09	0.31	0.22	0.13
Contribution	61.7%	17.8%	12.6%	7.4%

#### CDA ordination of habitats

Six variables (WL, pH, and concentrations of TDN, NH<sub>4</sub>-N, TDP and Fe) were employed in the CDA, which revealed four canonical functions that discriminated significantly between habitats of the six *Carex* species ( $p < 0.05$  by chi-square test) and, in total, explained more than 99% of the differences (Table 4). The first canonical function, which contributed over

60% to the difference, had the largest standardized coefficient for pH, followed by WL. This axis ordered species from the fen (*C. lyngbyei* and *C. thunbergii*), through the three common in fens and bogs, to the bog species (*C. middendorffii*); values correspond to the floristic variation between fen sites and bog sites (Fig. 2).

TDN concentration had a large positive coefficient, and Fe concentration a large negative one, in the second canonical function (nearly 20% contribution), and scores decreased from *C. lyngbyei*, the most productive species, to *C. limosa*, the least. The third canonical function was negatively related to TDN concentration and positively to TDP and gave lower scores to the habitats occupied by *C. thunbergii*. The contribution of the fourth canonical function was negligible. Overall, pH was the most strongly discriminating factor between the habitats of the six *Carex* species, followed by TDN concentration irrespective of pH.

#### Distribution along gradients of acidity and nitrogen richness

The least productive species, *C. limosa*, which grows in both fens and bogs, was distributed widely across acidic and neutral conditions, but was almost confined to N-poor habitats (TDN < 0.75 mg L<sup>-1</sup>, Fig. 3). The next less productive species, *C. middendorffii*, which grows only in bogs, was restricted to acidic conditions (pH < 5.5), and was mostly found at moderate TDN

levels (0.5-1.0 mg L<sup>-1</sup>). *C. lasiocarpa* and *C. pseudocuraica*, which are found mostly in fens, but also, sporadically, in bogs, showed skewed distributions between N-poor and weakly acidic sites and N-rich and acidic sites. Productive species such as *C. lyngbyei* and *C. thunbergii* were extensively distributed in N-rich habitats (TDN > 1.0 mg L<sup>-1</sup>), but were found only in those fens with weakly acidic conditions (pH > 5.0). The difference in pH between fen and bog sites was

significant: 5.91 ± SE 0.04 (n = 183) for fens and 4.59 ± 0.04 (n = 87) for bogs (t = 19.61, p < 0.0001), but the difference in TDN concentration was not significant, (0.62 ± 0.03 mg L<sup>-1</sup> vs 0.68 ± 0.03 mg L<sup>-1</sup>, t = 1.12, p = 0.265).

**Variation in calcium and magnesium concentrations**

Concentrations of Ca and Mg in the soil water were extremely low (mostly less than 5 mg L<sup>-1</sup> throughout the

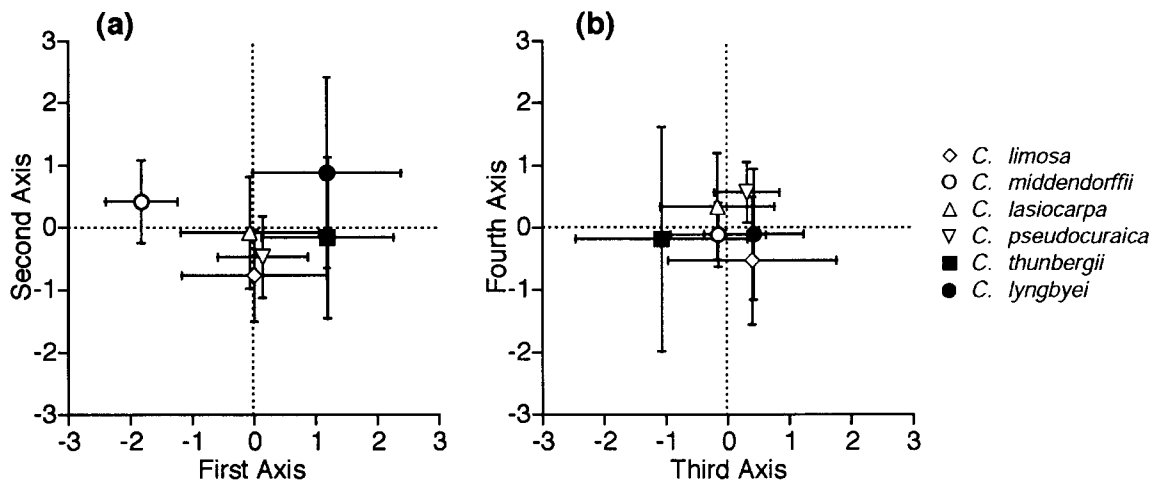


Fig. 2. Arrangement of mean scores for the first two canonical functions (A) and next two canonical functions (B) by CDA, with range bars showing SD.

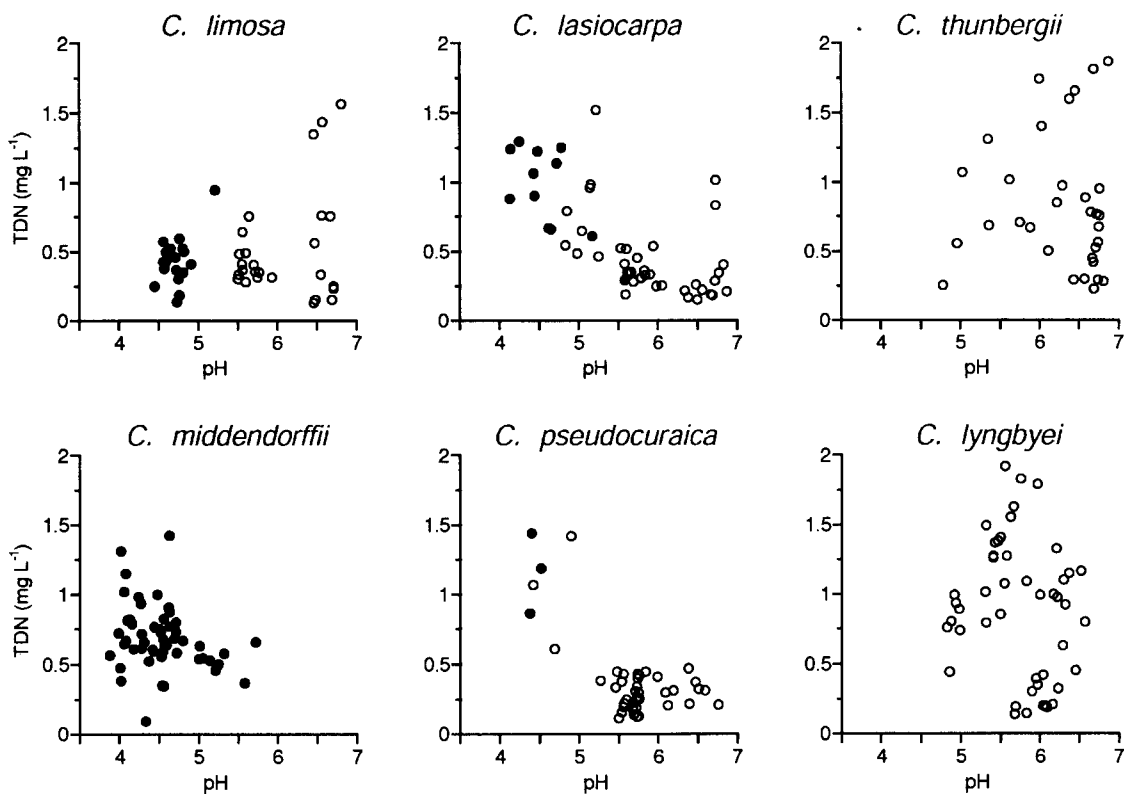


Fig. 3. Scatter plots of the six *Carex* species along the gradients of pH and TDN concentration in soil water with the vegetation type of each site, viz. open circles for fen and solid circles for bog.

range of pH, Fig. 4). Ca concentrations showed more variation in fen sites, although, overall, there was clear correlation with pH (Pearson's correlation coefficient  $r = 0.458$ ,  $p < 0.001$ ,  $n = 270$ ). The range of Mg was again slightly wider than in fen sites, but the correlation with pH was negative ( $r = -0.155$ ,  $p < 0.05$ ).

**Intra- and interspecific variation in nitrogen use traits**

The variations in NUE with soil water chemistry were similar to those in MRT (Fig. 5). Productive species such as *C. lyngbyei* and *C. thunbergii* had relatively small values of NUE and MRT, which were exceeded by those of the intermediately productive *C.*

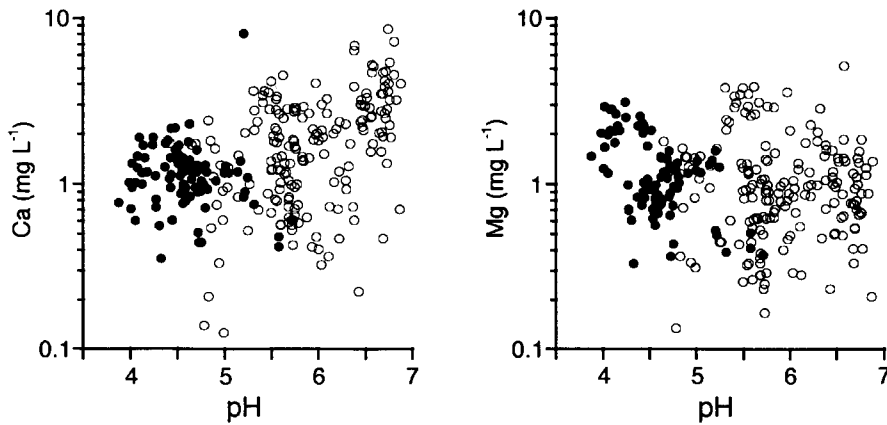


Fig. 4. Variation in concentrations of Ca and Mg versus pH in soil water. Symbols as in Fig. 3.

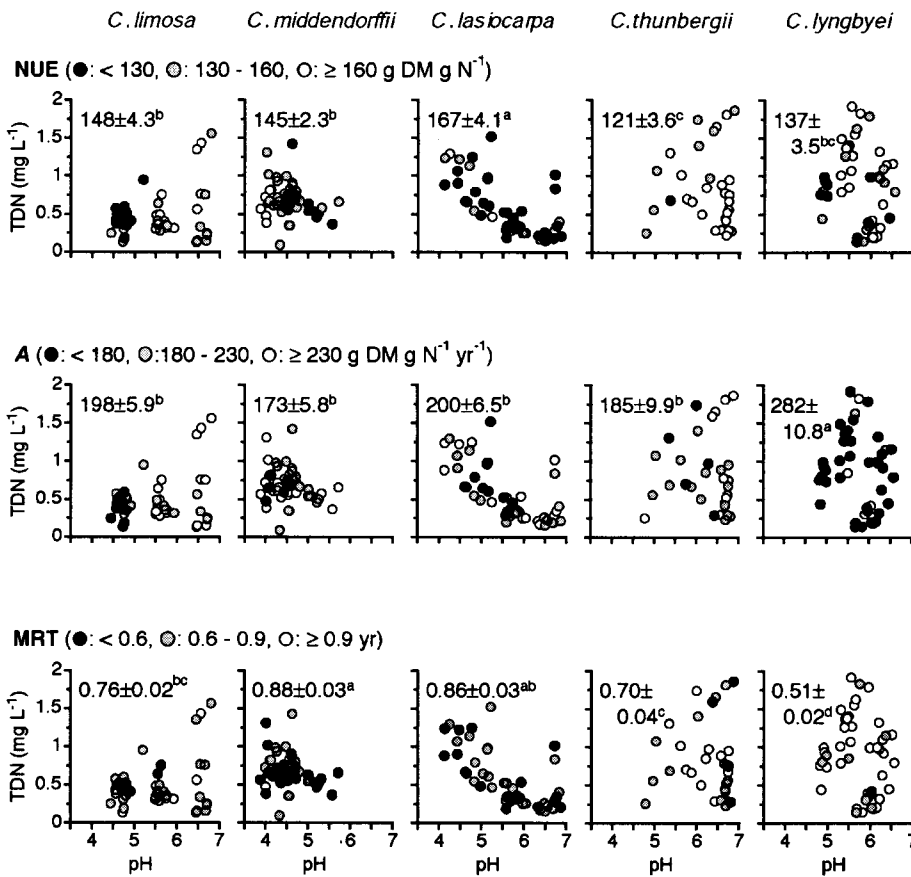


Fig. 5. Intraspecific variations in nitrogen use efficiency (NUE), nitrogen productivity (A) and mean residence time of nitrogen in the plant (MRT) in relation to pH and total dissolved nitrogen (TDN) in soil water. Symbols with different shading represent data in one of three classes: high, solid circles; intermediate, shaded circles; low, open circles. Means (± SE) NUE, A and MRT are shown for each species. Means followed by different letters are significantly different at  $p < 0.05$  (Scheffe's multiple-comparison test).

*lasiocarpa* and the less productive *C. middendorffii*. The least productive species, *C. limosa*, had intermediate values of NUE and MRT. The largest mean value of *A* occurred in the most productive species, *C. lyngbyei*, but there was no statistically significant difference in *A* among the other four species.

NUE and *A* of *C. limosa* and NUE of *C. thunbergii* correlated negatively with soil water acidity, while NUE of *C. middendorffii* correlated positively (Table 5). However, there were no significant correlations between any N use trait and TDN for any species.

Table 5. Correlation coefficients between each N use trait (NUE, *A* and MRT) and pH or TDN in the soil water. \*:  $p < 0.01$ , \*\*:  $p < 0.001$ .

		pH	TDN
<i>C. limosa</i> ( <i>n</i> = 46)	NUE	-0.620**	-0.122
	<i>A</i>	-0.608**	-0.242
	MRT	-0.036	0.107
<i>C. middendorffii</i> ( <i>n</i> = 51)	NUE	0.478**	-0.003
	<i>A</i>	-0.111	0.126
	MRT	0.304	-0.131
<i>C. lasiocarpa</i> ( <i>n</i> = 49)	NUE	-0.201	0.107
	<i>A</i>	-0.279	0.183
	MRT	0.159	-0.117
<i>C. thunbergii</i> ( <i>n</i> = 32)	NUE	-0.481*	0.243
	<i>A</i>	-0.368	0.003
	MRT	0.173	0.204
<i>C. lyngbyei</i> ( <i>n</i> = 46)	NUE	-0.156	-0.375
	<i>A</i>	-0.148	-0.230
	MRT	0.042	-0.046

*A* did not correlate significantly with either pH or TDN, whereas NUE and MRT increased as TDN decreased at weakly acidic (pH > 5.0) sites (Fig. 6). However, NUE and MRT at acidic sites (pH < 5.0) always significantly exceeded those at weakly acidic sites regardless of the TDN concentration (Table 6). *A* did not differ between strongly and weakly acidic sites.

Table 6. Mean ( $\pm$  SE) NUE, *A* and MRT in the *Carex* species growing in acidic and weakly acidic sites. Differences between means were compared using Students' *t* test. \*:  $p < 0.01$ , \*\*:  $p < 0.001$ .

	pH < 5.0	pH $\geq$ 5.0	<i>t</i>
NUE (g DM g N <sup>-1</sup> )	156 $\pm$ 0.3	139 $\pm$ 0.2	4.80**
<i>A</i> (g DM g N <sup>-1</sup> yr <sup>-1</sup> )	206 $\pm$ 0.7	210 $\pm$ 0.5	0.44
MRT (yr)	0.81 $\pm$ 0.002	0.72 $\pm$ 0.002	3.05*
<i>n</i>	82	142	

Aboveground biomass and N content of green plants in July were greater in weakly acidic sites compared with those in acidic sites (Table 7). They increased with TDN concentration at weakly acidic sites, but this trend was less obvious in acidic sites (Table 8).

Table 7. Mean ( $\pm$  SE) aboveground biomass and N content of green part of plants (July) growing in acidic and weakly acidic sites. Differences between means were compared using Students' *t* test (\*:  $p < 0.0001$ ).

	pH < 5.0	pH $\geq$ 5.0	<i>t</i>
Aboveground biomass			
shoot (g DM shoot <sup>-1</sup> )	0.43 $\pm$ 0.05	1.00 $\pm$ 0.10	4.36*
area (g DM m <sup>-2</sup> )	146 $\pm$ 9.2	304 $\pm$ 20.5	5.65*
N content			
shoot (mg N shoot <sup>-1</sup> )	4.57 $\pm$ 0.43	10.59 $\pm$ 0.95	4.64*
area (g N m <sup>-2</sup> )	1.72 $\pm$ 0.11	3.37 $\pm$ 0.21	5.68*
<i>n</i>	82	142	

Table 8. Correlation coefficients of aboveground biomass and N content of green plants with TDN concentrations in acidic and weakly acidic sites. (\*:  $p < 0.05$ , \*\*:  $p < 0.001$ , \*\*\*:  $p < 0.0001$ ).

	pH < 5.0	pH $\geq$ 5.0
Aboveground biomass		
shoot	0.211	0.311**
area	0.090	0.388***
N content		
shoot	0.232*	0.308**
area	0.043	0.373***
<i>n</i>	82	142

## Discussion

### Hydrochemical features of ecological gradients in mire vegetation

CDA clearly indicates that, of the factors considered, soil water pH is the most significant for the distribution of common *Carex* species in north Japanese mires. This supports general observations regarding pH conditions in fen and bog in Euramerican mires (e.g. Waughman 1980, Vitt *et al.* 1995, Wells 1996). Although the TDN concentration proved to be the next most important discriminating factor, the ordering of individual species according to their productivity was less clear, because of the widely overlapping ranges. Also, there was no obvious difference in TDN between fens and bogs, so that bog is not necessarily poorer in nutrients, as also recorded in Euramerican mires (Verhoeven *et al.* 1988, Verhoeven *et al.* 1990, Vitt *et al.* 1995).

Figure 7 schematically shows the distribution patterns of the six *Carex* species in these north Japanese

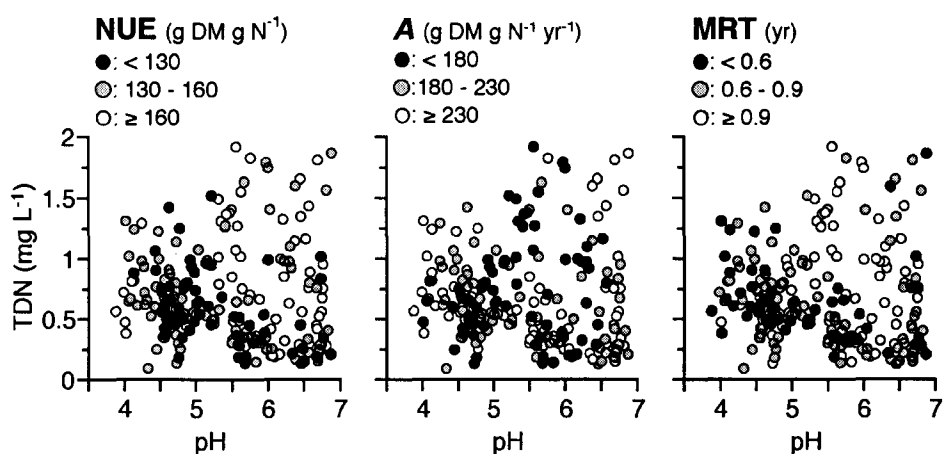


Fig. 6. Combined variations for all five *Carex* species in nitrogen use efficiency (NUE), nitrogen productivity ( $A$ ) and mean residence time of nitrogen in the plant (MRT) in relation to pH and total dissolved nitrogen (TDN) in soil water. Symbols as in Fig. 5. For  $\text{pH} \geq 5.0$ ,  $R = -0.237$  ( $p < 0.01$ ) for NUE, and  $R = -0.246$  ( $p < 0.01$ ) for MRT. No other correlations were statistically significant.

mires with respect to both pH and N richness. In weakly acidic sites, eutrophic and mesotrophic habitats are dominated by the more productive species such as *C. lyngbyei* and *C. thunbergii*, with the less productive species clearly restricted to oligotrophic habitats (*C. limosa*, *C. lasiocarpa* and *C. pseudocuraica*) or absent (*C. middendorffii*). In acidic sites, only middle to less productive species occur and their distribution is related to nitrogen richness, with the less productive species in more oligotrophic habitats. Overall, the difference in habitat preference of the species along the nutrient gradient strongly correlates with their productivity both in fens and bogs, except that eutrophic and mesotrophic fens were not distinguished.

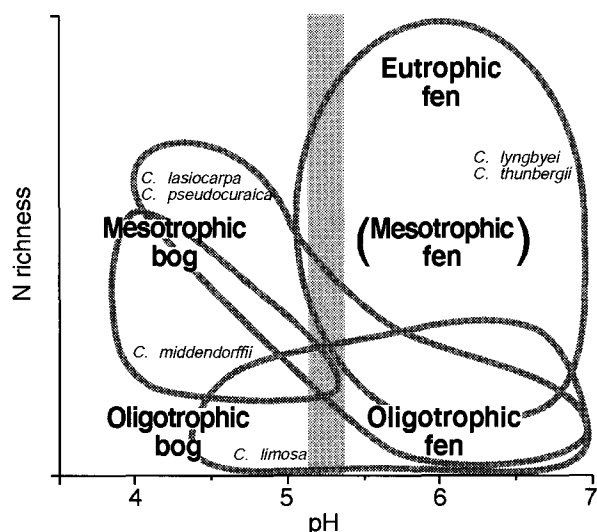


Fig. 7. Approximate boundary zone between fen and bog, and proposed arrangement of mire types along gradients of pH and N richness in the soil water, based on aboveground biomass and habitat preferences of *Carex* species.

Mesotrophic habitats in acidic sites, normally dominated by *C. lasiocarpa* and occasionally by *C. middendorffii*, correspond floristically to what has been described as poor fen (Malmer 1986). According to Wheeler and Proctor (2000), poor fen, usually covered by variable amounts of sphagna, should be classified as mesotrophic bog. However, poor and rich apply only to mires with calcareous vegetation, and therefore those habitats dominated by middle productive sedges associated with sphagna were designated as mesotrophic bog (rather than poor fen).

Wide ranges of Ca concentration, (up to more than  $200 \text{ mg L}^{-1}$  in NW European mires, Wheeler and Proctor 2000), have been thought to determine the pH of soil water (Du Rietz 1949, Wassen *et al.* 1989, Malmer *et al.* 1992, Bridgham *et al.* 1996). In Euramerican mires, such diversity in base richness, which is associated with pH, is indeed an important determinant of the floristic gradient (Waughman 1980, Malmer 1986, Vitt and Chee 1990). However, in boreal Fennoscandia, relatively low acidities are often found in those parts of silicious mires with low metal ion concentrations (Sjörs 1952). In Hokkaido, it has been speculated that Mg, which leaches out from underlying tephra, contributes to alkalization in ombrotrophic habitats, and plays a similar role to Ca in many Euramerican rich fens (Wolejko and Ito 1986). In the present study, the concentrations of Ca and Mg were consistently quite low (less than  $5 \text{ mg L}^{-1}$ ) at every pH. Habitats of fen species nevertheless differed clearly along the pH gradient from those of bog species, indicating that pH is a more appropriate discriminator between fen and bog than base richness.

Nitrogen levels in the habitats for *C. lasiocarpa* and *C. pseudocuraica* differed between fens and bogs, suggesting that specific nutrient availability for wetland plants probably changes as a result of habitat pH. Due to the recent deposition of air-borne pollutants, the P richness and alkalinity should correlate more strongly

with the floristic variation in nitrogen saturated mires (Økland *et al.* 2001), since P limitation on plant growth replaces N limitation (Aerts *et al.* 1992). In contrast with TDN, TDP did not contribute significantly to the difference between habitats of the *Carex* species, indicating that P limitation has not yet influenced floristic variation in north Japanese mires.

The pH of north Japanese mires may be more strongly affected by variation in components such as humic acids, rather than by base minerals. This is because their development is promoted primarily by frequent flooding with neutral water, which removes acid fractions, irrespective of base minerals (Yabe and Onimaru 1997). Although N richness in the soil water is not strictly comparable with the phytometric estimates of substratum fertility used as an index of nutrient status by Wheeler and Proctor (2000), nutrient variables contribute significantly to the ecological classification of plant productivity within fens and bogs. The two-variable model, based on pH and N richness, consequently extends Wheeler and Proctor's (2000) classification to north Japanese mires.

#### Variation in nitrogen use traits within and between *Carex* species

The results on plant N use traits can be summarised as follows:

- (1) Species such as *C. limosa* and *C. lasiocarpa* with large NUEs usually dominated N-poor habitats. Those with smaller NUEs (e.g. *C. lyngbyei* and *C. thunbergii*) dominated N-rich habitats.
- (2) At acidic sites, NUE was always high regardless of the TDN concentration, and trends in MRT were similar to those for NUE.
- (3) No significant correlations between *A* and TDN concentrations were found.
- (4) The N content and aboveground biomass of green plants evidently reflected the TDN concentration in weakly acidic habitats, but were not obviously correlated and were much lower in acidic habitats.

These results indicate that differences in NUE and habitat preference among the *Carex* species in weakly acidic conditions were generally as predicted (Chapin 1980, Vitousek 1982). However, variations in *A* and MRT among habitats did not always conform to the predictions of Berendse and Aerts' (1987) model.

Some of N-rich sites were dominated by productive species such as *C. thunbergii* with small *A* values (Fig. 5). Other N-rich sites were dominated by plants such as *C. lyngbyei* with large *A* values. The lack of a positive association between *A* and habitat fertility may be because *A* is simply the inverse of plant N concentration. Any dilution of plant N caused by large increases in biomass could, in theory, be compensated should sufficient N be available for uptake. This would effectively 'uncouple' *A* from the N supply of the habitat and explain the weak response of *A* to variations in TDN concentration (Tables 5, 6). The results suggest that large *A* is not necessarily advantageous for plants to dominate N-rich habitats. According to Berendse and

Aerts (1987), however, plants that are ecologically successful in N-rich habitats are more likely to have large *A* values.

In weakly acidic habitats MRT and NUE varied inversely with N content in the green plants. *Carex* species with longer MRT and larger NUE dominated N-poor habitats (Fig. 6). This combination of traits would minimise N loss if N uptake were limited. Potentially productive species, e.g. *C. lyngbyei* and *C. thunbergii*, had shorter MRT and smaller NUE, and such species dominated N-rich habitats. The possible advantages of short MRT to potentially productive species in fertile environments have not previously been considered. Variations in MRT are affected by leaf longevity (Escudero *et al.* 1992), as well as by nutrient resorption. A short MRT may primarily reflect short leaf longevity, and this can increase a plant's photosynthetic capacity if its canopy contains a large proportion of young, short-lived leaves (Chapin 1980). A short MRT in N-rich habitats would also maximise leaf N concentration (and, hence, photosynthesis) throughout the growing season by minimising N resorption. This could competitively favor plants with short MRT in N-rich habitats.

Inorganic N concentrations and mineralization rates in acidic habitats are not generally different from those in weakly acidic habitats (e.g. Waughman 1980, Verhoeven *et al.* 1988, Verhoeven *et al.* 1990). Differences in plant N content among acidic and weakly acidic habitats suggest a physiological restriction on N uptake by low pH. Therefore, plants growing in acidic habitats would be under greater selective pressure to minimise N loss (longer MRT) regardless of TDN. This would explain the observed MRTs of *C. limosa*, *C. lasiocarpa* and *C. middendorffii*.

In previous field studies, interspecific differences in N use traits were examined in relation to plant life forms and their association with habitat fertility (e.g. Vitousek 1982, Chapin and Shaver 1989, Aerts 1990, Aerts *et al.* 1999). Long MRT was associated with evergreen leaves, and short MRT with deciduous leaves. In pot experiments, strong intraspecific variations of N use traits to nutrient availability have been observed (Aerts and De Caluwe 1994, Vazquez de Aldana and Berendse 1997). Yet, within each of the five *Carex* species in their natural habitats, neither MRT nor *A* correlated with TDN (Table 5).

The hypothesised trade-off between *A* and MRT along nutrient gradients has been confirmed only for plants with different leaf habits (Aerts 1990). As this study has shown, the trade-off is not always apparent among phylogenetically similar species that do not differ in leaf habit. Accordingly, the ecological significance of variations in plant N use traits can be fully understood only if ecophysiological and phylogenetic information is included in the analysis.

#### Conclusion

Ecophysiological performances of the *Carex* species broadly growing in the north Japanese mires were primarily controlled by pH in the soil water rather than N richness, and this supported the validity of the

Wheeler and Proctor's (2000) paradigm on the ecological relationship proposed in European mires inclusive of Hokkaido. The variation in pH considerably contributed to the discrimination between fens and bogs that was the most important gradient in mires, and subsequently N richness did to the subdivision each within them. The relationship between N use traits and the habitat preferences along the gradients of pH and N richness derived the ecological rationales of the vegetation through the ecophysiological performances of individual species.

Mire ecosystem is generally very sensitive to the change in hydrochemical environments by artificial disturbance such as acid rainfall, inflow of base cations (Ca and Mg) and/or nutrients, and disturbance of the hydrological regime relating with the variation in acidic fractions (exploitation of catchment area). Hydrochemical alterations could easily and seriously damage the original vegetation indirectly through the replacement of species composing of the vegetation.

The variations in N use traits of plants along acidity and N richness theoretically supported the relationship between distribution patterns of mire vegetation and hydrochemical environments, and indicates the significance and generality of fen-bog gradient. This apprehension would much contribute to essential knowledge and practical information for the conservation, rehabilitation and restoration of mires, and should be useful for the estimation of vegetation responses to possible alteration of hydrochemical environments in the future.

#### Acknowledgements

I would like to express my gratitude to Associate Profs. Shigeru Uemura and Kazuo Yabe for their guidance in course of this study and critical reading of the manuscript. Thanks are also due to Drs. Teruyuki Komatsu, Takayoshi Koike, Mitsuru Osaki, Futoshi Nakamura, Tsutomu Hiura, Takashi Kohyama and Kazuyuki Onimaru for helpful supports and valuable comments for this study. I appreciate the staff in Laboratory of Uryu Experimental Forest, Hokkaido University and in Plant Resource Research of Tokyo University of Agriculture, for their cooperation during this study.

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## Appendix

Mean ( $\pm$  SE) aboveground biomass, N concentration and N content of green plants in July and dead plants in November.  $F$ -values obtained by ANOVA in each variable ( $p < 0.0001$  for all the variables). In different column, the same superscripts mean significant difference ( $p < 0.05$ , Scheffe's multiple-comparison test).

	<i>C. limosa</i> ( <i>n</i> = 46)	<i>C. middendorffii</i> ( <i>n</i> = 51)	<i>C. lasiocarpa</i> ( <i>n</i> = 49)	<i>C. thunbergii</i> ( <i>n</i> = 32)	<i>C. lyngbyei</i> ( <i>n</i> = 46)	<i>F</i> -value
Aboveground biomass						
Green (g DM shoot <sup>-1</sup> )	0.14 $\pm$ 0.01 <sup>c</sup>	0.32 $\pm$ 0.01 <sup>bc</sup>	0.47 $\pm$ 0.03 <sup>b</sup>	0.46 $\pm$ 0.03 <sup>b</sup>	2.54 $\pm$ 0.13 <sup>a</sup>	267.12
Green (g DM m <sup>-2</sup> )	87 $\pm$ 6.8 <sup>d</sup>	151 $\pm$ 8.4 <sup>cd</sup>	202 $\pm$ 16.4 <sup>bc</sup>	289 $\pm$ 24.9 <sup>b</sup>	527 $\pm$ 40.2 <sup>a</sup>	60.96
Dead (g DM shoot <sup>-1</sup> )	0.17 $\pm$ 0.01 <sup>c</sup>	0.36 $\pm$ 0.01 <sup>bc</sup>	0.49 $\pm$ 0.04 <sup>b</sup>	0.53 $\pm$ 0.04 <sup>b</sup>	3.26 $\pm$ 0.13 <sup>a</sup>	414.8
Dead (g DM m <sup>-2</sup> )	107 $\pm$ 7.2 <sup>c</sup>	170 $\pm$ 9.9 <sup>c</sup>	206 $\pm$ 17.3 <sup>bc</sup>	343 $\pm$ 35.3 <sup>b</sup>	693 $\pm$ 55.5 <sup>a</sup>	64.19
N concentration of shoot						
Green (%)	1.33 $\pm$ 0.03 <sup>a</sup>	1.34 $\pm$ 0.03 <sup>a</sup>	1.06 $\pm$ 0.02 <sup>b</sup>	1.32 $\pm$ 0.03 <sup>a</sup>	0.97 $\pm$ 0.02 <sup>b</sup>	46.33
Dead (%)	0.7 $\pm$ 0.02 <sup>b</sup>	0.7 $\pm$ 0.01 <sup>b</sup>	0.61 $\pm$ 0.01 <sup>c</sup>	0.85 $\pm$ 0.03 <sup>a</sup>	0.75 $\pm$ 0.02 <sup>b</sup>	20.96
N content						
Green (mg N shoot <sup>-1</sup> )	1.76 $\pm$ 0.09 <sup>c</sup>	4.24 $\pm$ 0.18 <sup>bc</sup>	4.88 $\pm$ 0.30 <sup>b</sup>	6.07 $\pm$ 0.43 <sup>b</sup>	24.96 $\pm$ 1.48 <sup>a</sup>	178.12
Green (g N m <sup>-2</sup> )	1.12 $\pm$ 0.09 <sup>c</sup>	2.02 $\pm$ 0.12 <sup>c</sup>	2.08 $\pm$ 0.16 <sup>c</sup>	3.83 $\pm$ 0.34 <sup>b</sup>	5.22 $\pm$ 0.44 <sup>a</sup>	43.49
Dead (mg N shoot <sup>-1</sup> )	1.18 $\pm$ 0.07 <sup>c</sup>	2.49 $\pm$ 0.11 <sup>bc</sup>	2.96 $\pm$ 0.24 <sup>bc</sup>	4.39 $\pm$ 0.26 <sup>b</sup>	24.96 $\pm$ 1.33 <sup>a</sup>	258.55
Dead (g N m <sup>-2</sup> )	0.77 $\pm$ 0.07 <sup>c</sup>	1.21 $\pm$ 0.08 <sup>c</sup>	1.26 $\pm$ 0.11 <sup>c</sup>	2.89 $\pm$ 0.31 <sup>b</sup>	5.43 $\pm$ 0.51 <sup>a</sup>	53.77