



## Biomass, species composition and diversity of epipellic algae in mire pools

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### Abstract

The biomass, species composition and diversity of epipellic algae in two small pools of contrasting physicochemical characteristics in Miyatoko Mire were studied in 1992 (pool 3 =site B4 and pool 50 =site D2). A total of 93 species and 67 species of epipellic algae occurred at sites B4 and D2, respectively. Considerable differences were observed between the two sites in the seasonal fluctuations of species number, biomass and dominant species. At site B4, little changed with species number during April–August and markedly increased in October, while biomass was largest in April and gradually decreased during June–October. Diatoms and desmids occupied 33–82% and 15–63% of total algal biomass, respectively. At site D2, species number and biomass were small in April just after the snow-thaw, and increased in June and decreased in August and October. Diatoms occupied 90–98% of total algal biomass. The species diversity was always higher at site D2 than B4. As a result of analyses of water chemistry in the two pools, pool B4 can be recognized as a habitat experiencing high disturbance frequency. It is predicted that pools experiencing frequent disturbance will have less epipellic algal biomass and diversity.

### Introduction

Mires, usually defined as unbalanced ecosystems in which an excess of organic matter produced by plants is only partly decomposed and the residues deposited as organic soil or peat (Masing et al., 1990), are important ecosystems for the conservation of biodiversity, because they have a variety of organisms endemic to these ecosystems. However, a number of mires have been fragmented or completely destroyed by human activities, such as drainage of ground water, peat extraction and land reclamation. An ecosystem approach based on both biological and hydrological studies is necessary for the conservation of these landscapes (Iwakuma, 1995).

In mires, algae are negligible as primary producers compared with *Sphagnum* moss, grasses and sedges, which are the dominant vegetation. However, it is gen-

erally recognized that algal species diversity in mires is very high and that there are many algal species endemic to mires (cf. Hirose & Yamagishi, 1977). Mires encompass running water systems, including pools of various sizes and physicochemical characteristics. The spatial and temporal heterogeneity of mire pools may powerfully influence algal community structure and diversity. However, there has been little quantitative study on algal community structure and environmental heterogeneity of pools in mires. Many of the previous studies on mire algae have been solely floristic, largely ignoring the community structure analyses (Hirano, 1942, 1943a,b; Lenzenweger, 1987; Kouwets, 1988).

As a part of ecosystem research on mires started in 1991, we studied the biomass, species composition and diversity of epipellic algae in two Miyatoko Mire pools of contrasting physicochemical characteristics in 1992. The present paper reveals quantitative characteristics of algal community structure and provides in-

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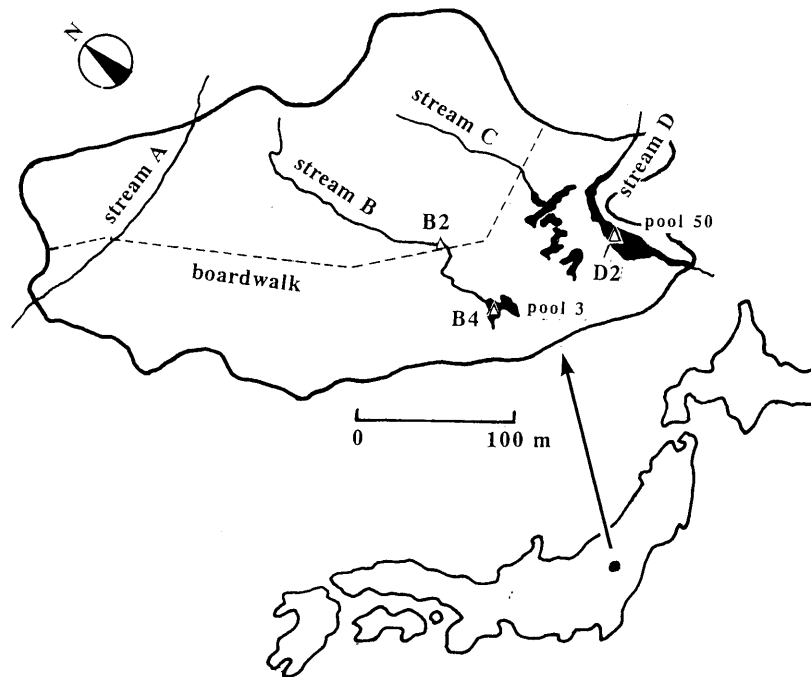


Figure 1. Study sites in Miyatoko Mire.

sights into the factors controlling the species diversity and biomass of epipellic algae in mires.

## Materials and methods

### Study site

Miyatoko Mire is located at latitude  $37^{\circ} 14' 48''$  N and longitude  $139^{\circ} 34' 6''$  E (Minami-Aizu, Fukushima Prefecture Japan) at an elevation of approximately 830 m above sea level. Stretching over a surface area of 6 ha, it is located between two mountains and mostly covered with *Sphagnum fuscum*, *S. magellanicum*, *S. palustre* and *S. papillosum* (Takehara, 1995). There are four streams crossing the mire, A, B, C and D (Figure 1). Streams A and D flow through the mire at opposite sites. The springs of these two streams rise out of the mire at opposite sites. The springs of streams B and C rise at the north-eastern and northern rims of the mire, respectively. Both streams are the runoff of ground water very close to the ground surface and are influenced by rainwater. About 50 pools are distributed in the south-eastern part of the mire where the elevation is low. Epipellic algal community structures were surveyed in Pool 3 (site B4) in stream B and Pool 50 (site D2) in stream D where only a few aquatic plants grow.

### Sampling and counting

In Miyatoko Mire, snowfall events were observed during November–April, and the mire surface was entirely covered with snow during December–March. Collections were made on 28 April, 22 June, 24 August and 1 October 1992. Epipellic algal samples were collected using a cylindrical syringe 14 mm in diameter: the syringe was set on the surface of sediment and then 6 ml sediment was collected. This procedure was repeated at 10 different points in each pool in order to incorporate any heterogeneity within the pool. All the samples from the 10 points were mixed and fixed by 2.5% glutaraldehyde. A total of 60 ml algal samples were collected from each pool on each collection date.

In the laboratory, 1 ml of each fixed-sample was diluted into 1/10 or 1/20. Apart from the diatoms, we identified the species and counted the cell number of each species using of Sedgwick-Rafter Counting Chamber under a light microscope. In the case of diatoms, an appropriate volume of each sample was boiled with  $H_2SO_4$  and  $KMnO_4$  and then washed in  $H_2O$ . An appropriate volume of the treated-sample was embedded in Pleurax. We identified most of diatoms with a light microscope and some small-sized ones with a SEM and counted the cell number for each species un-

der the light microscope. The counting was performed with four replicates for each sample to obtain mean and standard deviations. The cell volume of each algal species was calculated based on cell shape and size, and the carbon content of each algal cell was estimated according to the Strathmann equation (Strathmann, 1967).

#### Identification of algal species

Identification was carried out according to the following: Krammer & Lange-Bertalot (1986, 1988, 1991 a,b) for most diatoms, Kobayasi & Ando (1977) and Krammer (1992) for *Pinnularia*, Kobayasi & Nagumo (1988) for the small-sized species of *Navicula*, Mayama & Kobayasi (1990, 1991) and Kobayasi et al. (1981) for *Eunotia*, Patrick & Reiner (1966) for *Synedra* and some species of *Navicula*, Růžička (1977), Prescott (1984), Prescott et al. (1975, 1977, 1981, 1982) and Croasdale et al. (1983) for desmids, Geitler (1932) for blue-green algae, Huber-Pestalozzi (1941, 1955), Komárek & Fott (1983), Bourrelly (1972) and Starmach (1985) for the other algae.

#### Estimation of species diversity

The species diversity was estimated with Simpson's Diversity Index ( $D$ ) as follows.

$$D = 1 / \left[ \sum_{i=1}^s (n_i / N)^2 \right] \quad (\text{Simpson, 1949}),$$

where  $s$  is total species number,  $n_i$  is the number of individuals in the  $i$ -th species and  $N$  is the total number of individuals. Also, the modified diversity index,  $D'$ , was estimated based on biomass. In this case,  $n_i$  is the biomass of the  $i$ -th species and  $N$  is the total biomass of epipelagic algae.

## Results

### Algal flora

A total of 67 species of epipelagic algae, including 40 diatoms, 18 desmids and nine other algae, occurred at site B4 (Table 1). A total of 93 species of epipelagic algae, comprised of 65 diatoms, 15 desmids and 13 other algae, occurred at site D2 (Table 1). Twelve species occurred only at site B4 and only 39 species at site D2.

Table 1. Algal species occurred at Sites B4 and D2 in Miyatoko Mire. <sup>a</sup> Volume ( $\mu\text{m}^3$ ) calculated based on cell shape and size. <sup>b</sup> Carbon content ( $\text{pgC cell}^{-1}$ ) estimated according to Strathmann equation (1967)

Species	B4	D2	Volume <sup>a</sup>	Carbon content <sup>b</sup>
Diatoms				
<i>Achnanthes helvetica</i>		+	692	54
<i>A. minutissima</i>	+	+	70	10
<i>A. nodosa</i>		+	84	11
<i>A. pusilla</i>	+	+	188	20
<i>A. subatomoides</i>		+	94	12
<i>Actinella punctata</i>	+	+	3815	196
<i>Anomoeoneis brachysira</i>	+	+	218	22
<i>A. serians</i> var. <i>acuta</i>	+	+	1620	103
<i>Aulacoseira alpigena</i>	+	+	500	42
<i>A. canadensis</i>		+	921	67
<i>A. laevissima</i>		+	1177	80
<i>A. valida</i>		+	2849	157
<i>Cymbella gracilis</i>	+	+	500	42
<i>C. minuta</i>	+	+	302	29
<i>C. naviculiformis</i>		+	3327	177
<i>C. sinuata</i>	+		150	17
<i>Eunotia curvata</i>	+	+	367	33
<i>E. curvata</i> var. <i>linearis</i>	+	+	2500	142
<i>E. diadema</i>		+	12716	489
<i>E. exigua</i>	+	+	506	42
<i>E. incisa</i>		+	384	34
<i>E. naegeli</i>	+	+	262	26
<i>E. nipponica</i>	+	+	7000	311
<i>E. parallela</i>	+		3240	173
<i>E. pectinalis</i> var. <i>minor</i>	+	+	595	48
<i>E. perminuta</i>		+	113	14
<i>E. rhomboidea</i>	+		153	17
<i>E. serra</i>	+	+	28138	892
<i>E. tenelloides</i>	+	+	100	12
<i>Fragillaria capucina</i> var. <i>gracilis</i>	+	+	100	13
<i>F. construens</i> var. <i>venter</i>	+		137	16
<i>F. elliptica</i>		+	69	9
<i>F. exigua</i>		+	132	15
<i>F. nitzschoides</i>		+	435	38
<i>F. sp.</i>		+	1377	91
<i>Frustulia rhomboides</i>	+	+	35332	1061
<i>F. rhomboides</i> var. <i>saxonica</i>	+	+	5070	243
<i>Gomphonema accuminatum</i>	+		2301	134
<i>G. garacile</i>		+	425	37
<i>G. parvulum</i>	+	+	287	28
<i>Meridion circulare</i>	+	+	750	57
<i>Navicula mediocris</i>	+	+	75	10

Continued on p. 94

Table 1. Continued

Species	B4	B2	Volume <sup>a</sup>	Carbon content <sup>b</sup>
<b>Diatoms</b>				
<i>N. minima</i>		+	138	16
<i>N. minuscula</i>		+	126	15
<i>N. notha</i>		+	537	44
<i>N. okadae</i>	+	+	1012	72
<i>N. parasubtilissima</i>	+	+	303	29
<i>N. pseudosctiformis</i>		+	699	54
<i>N. seminulum</i>		+	157	17
<i>N. subtilissima</i>	+	+	522	43
<i>Neidium iridis</i>		+	95062	2246
<i>Nitzschia amphibia</i>	+	+	225	23
<i>N. fontinalis</i>		+	76	10
<i>N. hantzschiana</i>		+	153	17
<i>N. palea</i>	+	+	450	39
<i>Peronia fibula</i>	+	+	400	36
<i>Pinnularia bogotensis</i>		+	35840	1072
<i>P. hilseana</i> var. <i>japonica</i>	+	+	4096	207
<i>P. microstauron</i>		+	28977	913
<i>P. subgibba</i>		+	14400	537
<i>P. transversa</i>	+		64000	1664
<i>P. viridis</i>	+	+	53802	1459
<i>Stauroneis phoenicenteron</i>		+	77824	1930
<i>Stenopterobia curvula</i>	+	+	5112	245
<i>S. delicatissima</i>	+	+	1600	102
<i>Surirella linearis</i>		+	39865	1162
<i>Synedra acus</i>		+	2238	131
<i>S. ulna</i>	+	+	2767	154
<i>Tabellaria fenestrata</i>	+	+	2615	147
<i>T. flocculosa</i>	+	+	808	61
<b>Green Algae: Desmids</b>				
<i>Bambusina brebissonii</i> var. <i>brebissonii</i>	+	+	8079	832
<i>Closterium acerorum</i>		+	34605	2951
<i>C. acutum</i> var. <i>acutum</i>	+		1415	186
<i>C. costatum</i>		+	196250	13291
<i>C. gracile</i>		+	1695	219
<i>C. intermedium</i>	+	+	15272	1445
<i>C. lunula</i>		+	847800	46774
<i>C. parvulum</i> var. <i>maius</i>		+	32708	2818
<i>C. peracerosum</i>		+	5652	617
<i>Cosmarium angulare</i> var. <i>angulare</i>	+		5128	566
<i>Cylindrocystis crassa</i>		+	12560	1230
<i>Euastrum crassum</i> var. <i>tumidum</i>	+	+	524160	31121
<i>E. didelta</i> var. <i>didelta</i>	+		62694	4948
<i>Gloenblanda neglecta</i> var. <i>neglecta</i>	+	+	2653	320

Table 1. Continued

Species	B4	B2	Volume <sup>a</sup>	Carbon content <sup>b</sup>
<b>Green Algae: Desmids</b>				
<i>Mesotaenium degreyi</i> var. <i>breve</i>	+		7771	811
<i>Micrasterias apiculata</i> var. <i>apiculata</i>	+		296503	19001
<i>M. denticulata</i>	+		318396	20210
<i>M. truncata</i>	+		63842	5026
<i>Netrium digitus</i> var. <i>digitus</i>	+	+	77507	5945
<i>N. digitus</i> var. <i>naegeli</i>	+		9272	945
<i>Pleurotaenium minutum</i> var. <i>crassum</i>	+		105855	7788
<i>P. minutum</i> var. <i>minutum</i>	+	+	15045	1438
<i>P. undulatum</i> var. <i>undulatum</i>	+	+	19040	1763
<i>Staurastrum geminatum</i>	+	+	5333	586
<i>S. micron</i> var. <i>micron</i>	+		533	78
<b>Green Algae: Others</b>				
<i>Bulbochaete</i> sp.	+		12650	1229
<i>Gloeoitila turfosa</i>		+	78	15
<i>Klebsormidium klebsii</i>	+	+	769	109
<i>Microspora willeana</i>		+	1177	158
<i>Oedogonium</i> sp.	+		35325	3011
<i>Pediastrum boryanum</i>		+	1766	225
<i>Scenedesmus acutus</i>	+	+	98	18
<b>Blue-green Algae</b>				
<i>Anabaena</i> sp.	+	+	523	78
<i>Chroococcus turgidus</i>	+	+	1766	225
<i>Merismopeida glaucum</i>		+	65	13
<i>Oscillatoria</i> sp.	+	+	12	3
<i>Stigonema ocellatum</i> f. <i>ocellatum</i>	+		523	78
<b>Other Algae</b>				
<i>Dinobryon sertularia</i>		+	3532	410
<i>Gymnodinium</i> sp.		+	6280	675
<i>Synula sphagnicola</i>		+	3532	410
<i>Trachelomonas</i> sp.	+	+	523	78

### Seasonal changes in total biomass and total cell number of epipelagic algae

The biomass of epipelagic algae at site B4 was highest in April, 4115 ng C mm<sup>-2</sup> and then gradually decreased from June to October, when the population was at its smallest, 1562 ng C mm<sup>-2</sup> (Figure 2). A similar pattern of seasonal change was observed for the total cell number.

The biomass of epipelagic algae at site D2 was 1190 ng C mm<sup>-2</sup> in April and had increased greatly by June, peaking at 5970 ng C mm<sup>-2</sup>. Biomass decreased

during the August–October period (see Figure 2). The same pattern of seasonal change was observed for total cell number. Except for April, algal biomass at site D2 was larger than that at site B4.

#### *Seasonal changes in biomass of each epipellic species*

At site B4, diatoms and the desmids comprised 73% and 26%, respectively, of total algal biomass in April (Figure 3). The biomass of diatoms decreased, but that of the desmids increased in June. The desmids comprised 63% of total algal biomass. The former had increased, but the latter had decreased by August. The diatoms occupied 82% of total algal biomass. The relative composition was similar in October. Diatoms plus desmids together comprised 96–99% of total algal biomass throughout the season. *Frustulia rhomboides* was the most dominant species in April, August and October, and predominated also in June together with the two desmid species, *Bambusina brebissonii* var. *brebissonii* and *Netrium digitus* var. *digitus* (Figure 4). Among the diatoms, only *Frustulia rhomboides* was prominent and comprised 65–96% of the diatom biomass throughout the season (Figure 4). In contrast, the prominent green algae differed from season to season: *Gloenblandia neglecta* var. *neglecta* in April, *Netrium digitus* var. *digitus* and *Bambusina brebissonii* var. *brebissonii* in June, *Gloenblandia neglecta* var. *neglecta* again in August, and *Micrasterias denticulata* var. *denticulata* in October (Figure 4). At site B4, *Frustulia rhomboides*, together with one or two desmid species, comprised 70–90% of total algal biomass throughout the season.

Diatoms predominated in every season and comprised 90–98% of total algal biomass at site D2 (Figure 3). Thus, site B4 is characterized by predominance of diatoms and desmids, while site D2 by predominance of only diatoms. The dominant species and their seasonal changes at site D2 differed from those of site B4 (Figure 5). No marked predominance of any species was observed in April. Although *Frustulia rhomboides* occurred with a relatively large biomass, it comprised only 10% of total algal biomass. A centric diatom, *Aulacoseira laevisima*, predominated and comprised approximately 40% total biomass in June. The other diatoms with a relatively large biomass were *Aulacoseira canadensis*, *A. alpigena*, *Eunotia serra* and *Pinnularia subgibba*. All were present in small numbers, or absent, in April. The total biomass of diatoms decreased in August, but *Aulacoseira laevisima* still predominated as in June and comprised

approximately 32% total algal biomass. Algal species composition changed markedly in October. *Actinella punctata*, *Stauroneis phoenicenteron* and *Pinnularia subgibba* occurred with a relatively large biomass, but no marked predominance of any species was observed in April. Diatoms, designated as other diatoms in Figure 5, occupied approximately 35–50% total algal biomass throughout the season (see Figure 5). This contrasts with site B4, where only *Frustulia rhomboides* and one or two desmids comprised 70–90% of the total biomass of epipellic algae. The biomass of green algae comprised only a few percent of the total biomass. The dominant species of these algae changed seasonally, being *Klebsormidium klebsii* in April, *Closterium lunula* in June, *Closterium parvulum* var. *maius* in August and *Closterium costatum* and *Pleurotaenium minutum* var. *minutum* in October (Figure 5).

#### *Species richness and diversity*

A total of 105 species of the epipellic algae were identified from the two pools: 67 at site B4 and 93 at site D2 (Table 1). At site B4, the total number of species was 29–32 during April–August, this increasing to 43 in October (Figure 6). This pattern did not correspond to those of biomass or total cell number (Figure 2). The diversity index estimated, based on cell number,  $D$ , was high in April, low in June and August and reached its maximum in October, and the pattern of its seasonal change from June–October corresponded to that of total number of species (Figure 6). However, the other index estimated based on biomass,  $D'$ , did not change much throughout the season and the pattern of its seasonal change during April–August corresponded to that of total species number (Figure 6).

At site D2, species number was 49 in April, increased to 60 in June and decreased to 54 in August and to 48 in October (Figure 6). This pattern corresponded to that of biomass (Figure 2). However, both diversity indices,  $D$  and  $D'$ , showed a pattern of seasonal change inverse to those of species number and biomass (see Figure 2). The species number and diversity indices of epipellic algae were higher at site D2 than at site B4 throughout the season.

## **Discussion**

Fifty four species of higher plants and mosses have been described in the Miyatoko Mire (Takehara,

Table 2. Summary of water chemistry statistics for sites D2 and B2 and tests of differences between sample variances based on the *F*-test. Mean ( $\bar{X}$ ), standard deviation (SD), sample variance ( $V$ ), and degree of freedom ( $df$ ). This table was made based on the data taken by Hirata et al. (1995)

	B2				D2				$F_0^a$	$F^b$
	$\bar{X}$	SD	$V$	$df$	$\bar{X}$	SD	$V$	$df$		
Temp.	20.36	8.24	8.49	8	12.90	3.32	1.38	8	6.15	4.43
pH	5.21	0.42	0.02	8	6.08	0.41	0.02	8	1.00	4.43
$\text{NH}_4^{+c}$	0.09	0.06	0.0004	9	0.05	0.04	0.0002	9	2.00	4.03
$\text{Cl}^-$	2.10	0.90	0.09	9	2.39	0.44	0.02	9	4.50	4.03
$\text{SiO}_2$	2.56	1.83	0.37	9	18.25	2.67	0.79	9	2.13	4.03
$\text{SO}_4^-$	2.81	0.55	0.033	9	1.33	0.63	0.044	9	1.30	4.03
$\text{Na}^+$	1.00	0.23	0.0059	9	2.11	0.29	0.0093	9	1.58	4.03
$\text{K}^+$	0.31	0.19	0.004	9	1.05	0.19	0.004	9	1.00	4.03
$\text{Mg}^{++}$	0.46	0.15	0.0025	9	0.28	0.05	0.0003	9	8.33	4.03
$\text{Ca}^{++}$	0.82	0.33	0.012	9	0.61	0.22	0.0054	9	2.22	4.03

<sup>a</sup> $F_0 = V_B/V_D$  or  $V_D/V_B$ .

<sup>b</sup>The value from *F* distribution table of  $F(df_D, df_B; 0.025)$  or  $F(df_B, df_D; 0.025)$ .

<sup>c</sup>Each ion concentration ( $\text{mg l}^{-1}$ ).

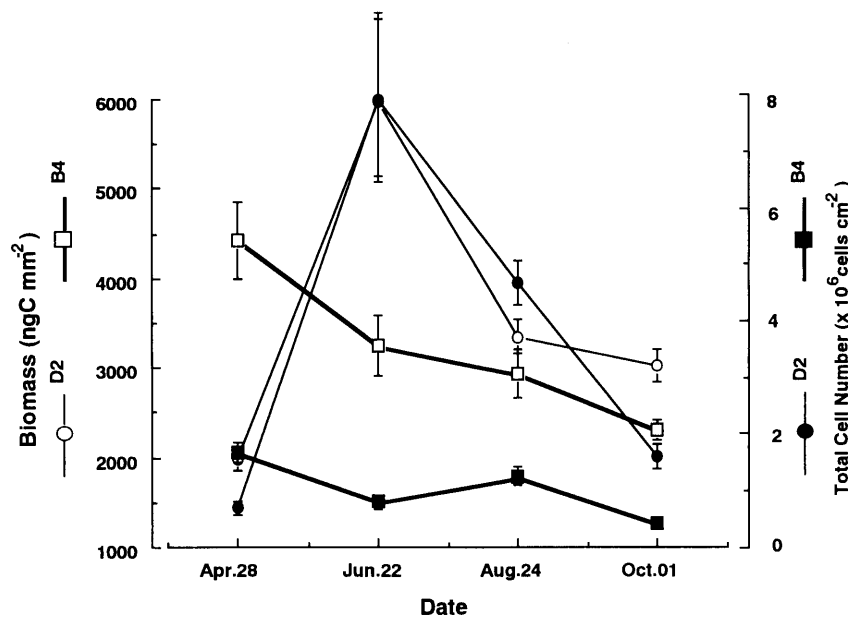


Figure 2. Seasonal changes in biomass and total cell number of epipellic algae at sites B4 and D2. Vertical bars show standard deviations.

1995), while 105 species of epipellic algae were found in two of the 50 pools distributed in the mire. From the physico-chemical data (mean values and standard deviations) of surface water monitored at site B2 near site B4 and at site D2 in the streams B and D (Hirata et al., 1995), there were great differences in water quality between sites B2 and D2, especially temperature and silicate concentration (Table 2). In addition, pH and concentrations of univalent cations, such as so-

dium and potassium, were significantly lower at site B2 than D2, while temperature and concentrations of sulfate and divalent cations, such as magnesium and calcium, were significantly higher at site B2 than D2. Standard deviations of water chemical determinands at both sites showed large values. We have also measured temperature and pH at site B4 on each collection date and the values were mostly identical to those at site B2. Thus, water quality at B2 can be treated as repre-

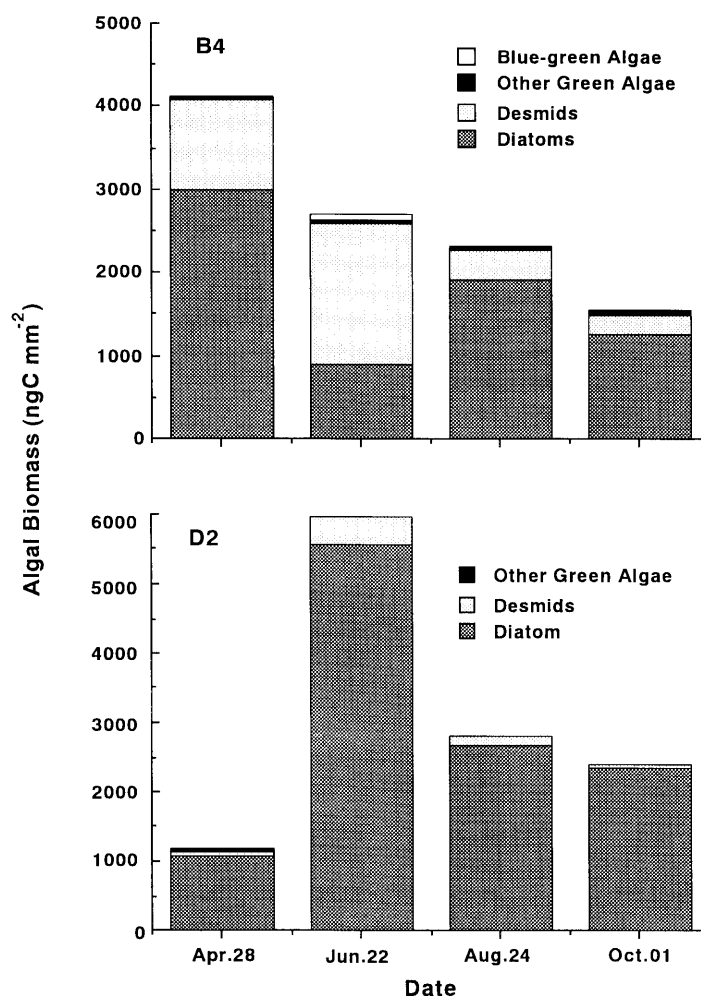


Figure 3. Seasonal changes in mean value of biomass of diatoms, desmids and other algae at sites B4 and D2.

representative of that at site B4. It is, therefore, suggested that the habitats of B4 and D2 differ greatly from each other and that the aqueous environment of these two sites fluctuated greatly from season to season. It seems that there are a number of pools with different habitats in Miyatoko Mire. On the other hand, the ground of the mire where higher plants and mosses grow is on the whole homogeneous and the vegetation is affected mainly by the level of ground water. According to Wiens (1976), habitat heterogeneity may be related to an increase in species diversity. It is suggested that habitat heterogeneity of the pools in the mire is responsible for the high diversity of epipelagic algae.

Site B4 is characterized by the predominance of diatoms and desmids and site D2 by the predominance of only diatoms (Figure 3). The water temperature of site D2 ranged from 8.9 °C to 17.8 °C (mean=12.8 °C), be-

ing much lower than that of site B2 which ranged from 9.7 °C to 30.9 °C (mean=20.36 °C) (see Table 2). The concentration of silicate at site D2 was in the range 11.7–20.4 mg l<sup>-1</sup> (mean=18.25 mg l<sup>-1</sup>), much higher than that of site B2 (0.5–6.2 mg l<sup>-1</sup>, mean=2.56 mg l<sup>-1</sup>). The lower temperature and high silicate concentration at D2 may result in the predominance of diatoms, while high temperature and low silicate concentration at B2 may lead to the predominance of both diatoms and desmids at B4, because diatoms require silicate for their growth and prefer low temperatures, while desmids do not require silicate for their growth and can grow at relatively high temperatures.

There have been a number of previous reviews of phytoplankton diversity (cf. Harris, 1986). In general, using a diversity index like  $H'$  (Shannon-Weaver diversity index) or  $D$ , phytoplankton diversity varies

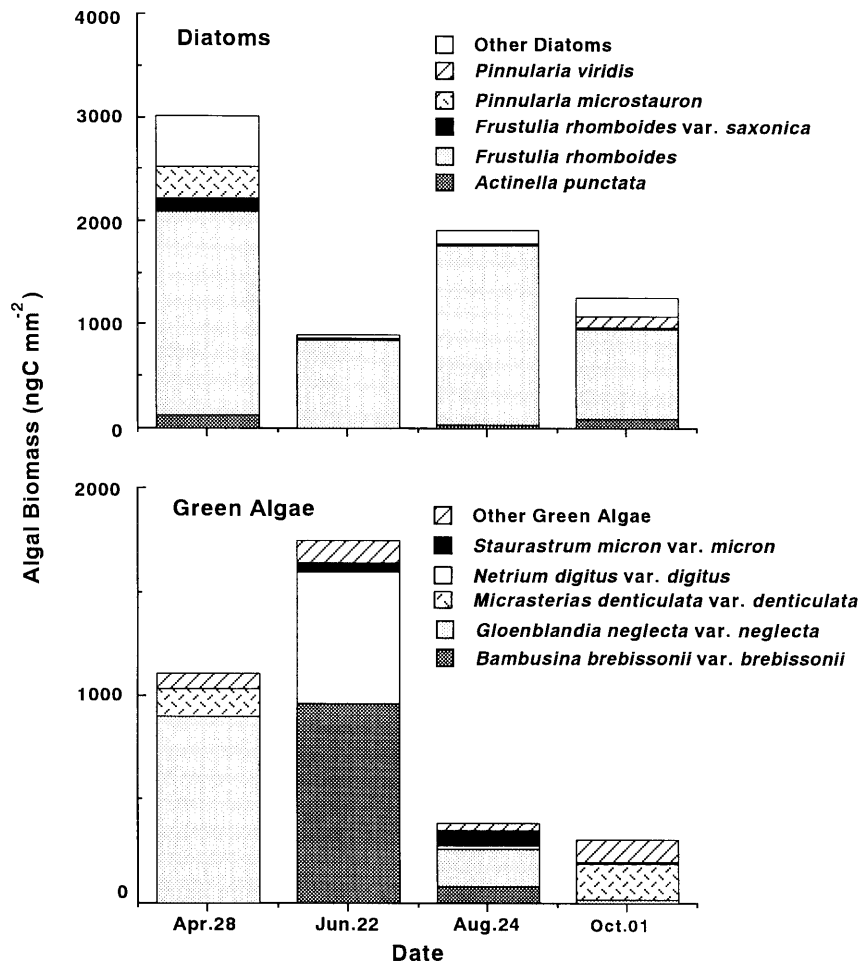


Figure 4. Seasonal changes in mean value of biomass of each diatom and green algal species at site B4.

with a strong seasonal component (Margalef, 1958). However, little is known concerning the diversity of epipelagic algae in mires. At Miyatoko Mire, the diversity of epipelagic algae showed seasonal variations, but the features of the two sites, B4 and D2, were quite different from each other. At B4, there was no clear relationship between the seasonal changes of species number, total biomass and total cell number, though the seasonal changes of diversity indices were partly related to that of total species number. Also, the patterns of seasonal change of the two diversity indices,  $D$  and  $D'$ , were different from each other. The difference between  $D$  and  $D'$  seems to be caused by a filamentous blue-green alga, *Oscillatoria* sp., which occurred in June and August. The filament of this species is composed of cells with approximately  $1 \mu\text{m}$  diameter and  $4 \mu\text{m}$  length. In June and August, this species com-

prised 50–54% of total cell number of epipelagic algae, but only 0.4–0.9% of total algal biomass. Hence, the diversity index  $D$  became low in June and August, but  $D'$  did not change throughout the season. At site B4, only *Frustulia rhomboides* and one or two desmid species occupied 70–90% of total biomass throughout the season, including October when the total number of species reached its maximum (Figures 4 and 6). These qualitative and quantitative features correspond to the pattern of seasonal change of  $D'$ . It is suggested that  $D'$  is a more suitable index of species richness and evenness in algae whose cell size differs markedly from species to species and that the diversity indices at B4 are related to both the total number of species and their relative abundance. At D2, seasonal changes in species number corresponded to those of biomass and total cell number (Figures 2 and 6). However, the



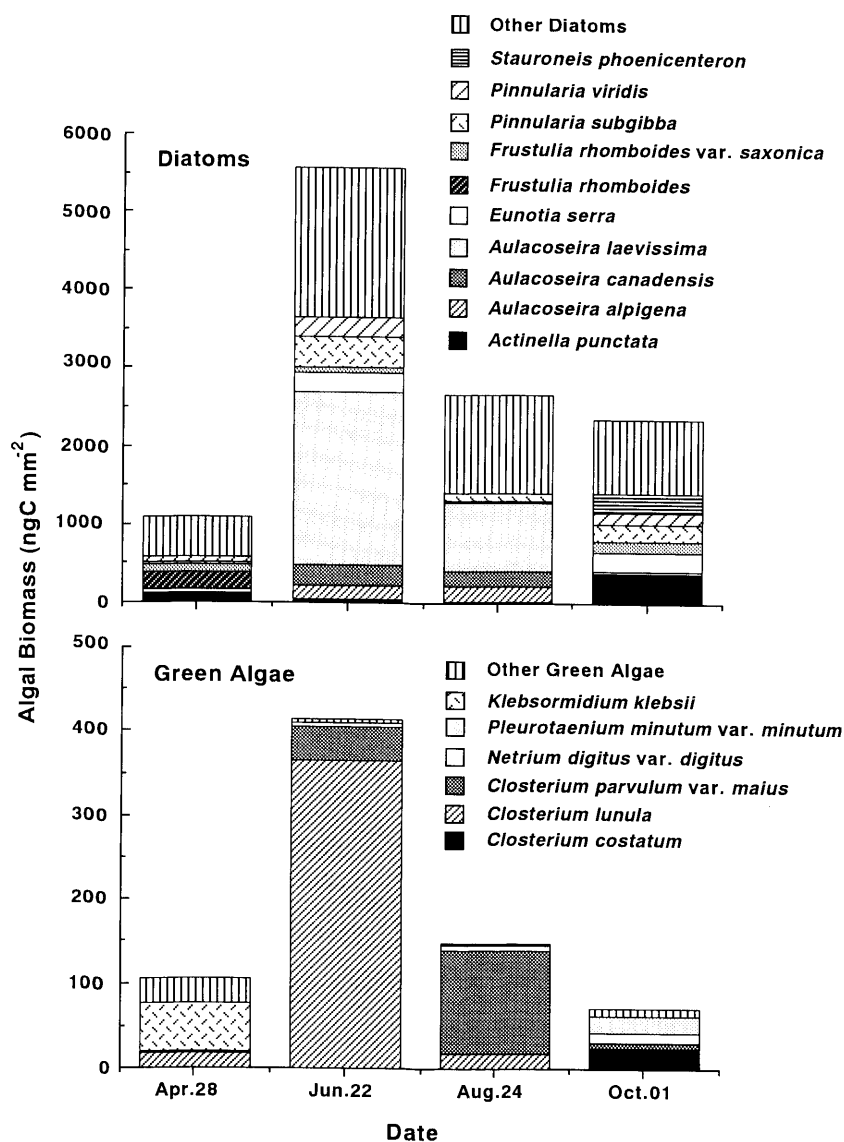


Figure 5. Seasonal changes in mean value of biomass of each diatom and green algal species at site D2.

seasonal changes of both diversity indices,  $D$  and  $D'$ , showed an inverse pattern to those of species number, biomass and total cell number. This means that species evenness greatly decreased with increasing size of algal population. *Aulacoseira laevissima* increased in biomass and occupied approximately 40% of total biomass in June when algal biomass and species number increased (cf. Figures 2, 5 and 6). The same was true in August when *A. laevissima* occupied about 32% total biomass. The decrease in values for the diversity indices at these seasons was probably caused by the high relative abundance of the dominant species. In

April and October, when both species number and size of algal population (=algal biomass) were small, the dominant species occupied only 10 or 16% of total biomass. Such a low relative abundance of dominant species result in increasing species evenness and high diversity indices. According to May (1975), the two common measures of diversity,  $H'$ , the Shannon-Weaver diversity index (cf. Margalef, 1958) and  $D$ , Simpson's index, are related to both the total number of species and their relative abundances, and can be designated as a positive function of total number of species. The same has been observed in the

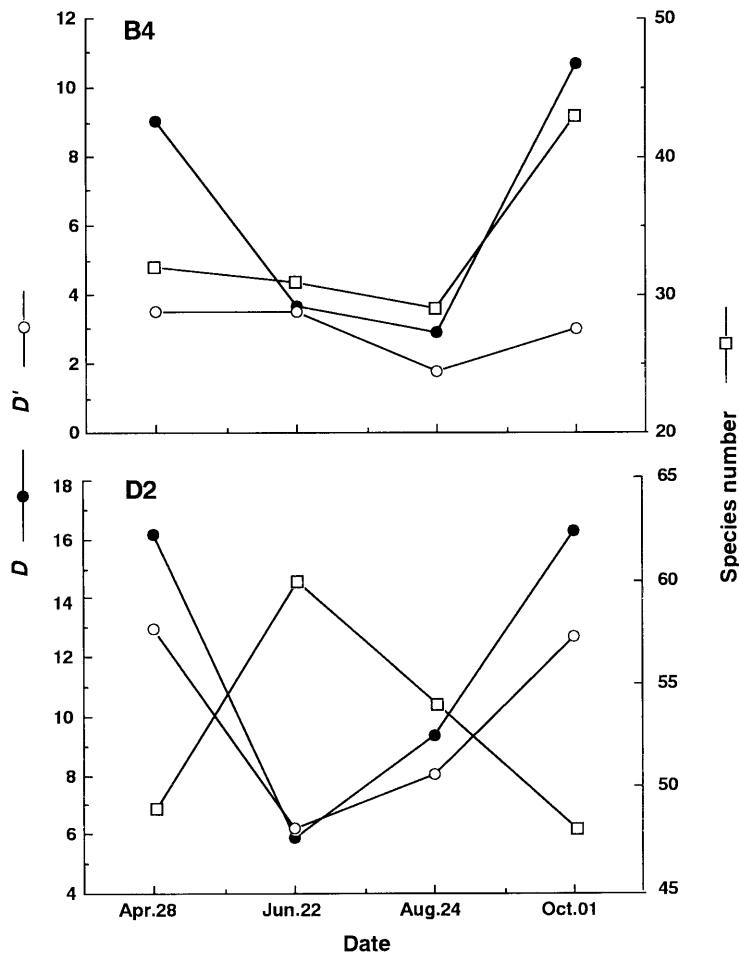


Figure 6. Seasonal changes in species number (mean) and diversity indices at sites B4 and D2.

marine phytoplankton community (cf. Harris et al., 1983). However, the Simpson's index at site D2 is strongly controlled by the relative abundance of dominant species and shows a negative relationship with total number of species. This was also true when the diversity at site D2 was measured using the Shannon-Weaver index,  $H'$  (data not shown). Further studies are needed to establish how diversity index,  $D$  or  $H'$ , are related to the total number of species and their relative abundances.

The species number and the diversity indices of the epipellic algae at D2 were higher than those at B4 throughout the season, meaning that the algal population at D2 has higher species richness and evenness than that at B4. This result seems to reflect the fact that just a few species comprised more than 70% total algal biomass throughout the seasons at B4, while no species comprised more than 50% total algal biomass

at D2. In addition to the high species richness and diversity, the biomass of epipellic algae at D2 was larger than that at B4 in any season except for April (Figure 2). As shown in Table 2, the concentration of silicate was much lower at B2 than D2. A silicate is practically absent in rain water and stream B is known to have a strong surface water flow influenced by rain water (Hirata et al., 1995). One year before the survey (1991), when there was little rain in summer, the water dried up almost all over the stream B and the water level of pool 3 (site B4) became very low. In 1992, the algal biomass at B4 was largest in April just after snow-thaw and decreased with the water volume fluctuating during rainy June to a hot summer. It seems that the site B4 experienced great disturbance throughout the seasons. In addition, from the  $F$ -test for difference in variance of water temperature and chemical determinands between the two sites, B2 and

D2, it was found that variations of temperature,  $\text{Cl}^-$  and  $\text{Mg}^{++}$  are significantly greater at B2 than at D2. This suggests that B4 is subject to higher disturbance frequency than D2.

A stream reach is influenced by physical events such as landslides and channel shifts and also pools are influenced by flood scour and deposition, drying up and thalweg shifts (cf. Scarsbrook & Townsend, 1993). So disturbance has been seen as a major structuring force in stream and pool communities (Resh et al., 1988; Reice et al., 1990). Resh et al. (1988) and Scarsbrook & Townsend (1993) suggested that streams experiencing frequent disturbance will have less biomass and diversity of epilithic algae than more stable streams. As shown before, both sites experience frequent disturbance, especially site B4, with less biomass and diversity of epipellic algae, is strongly influenced by flood scour and drying up and faced with high disturbance frequency. These results support their diversity-disturbance theory in the epipellic algal community.

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