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Research Report

Who killed the reed?
Mechanisms of vegetation change at
Kiritappu Mire, eastern Hokkaido

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1. Introduction

During the last 50 years drastic vegetation changes have occurred along the middle reaches of Ichibangawa River in the southern part of Kiritappu Mire (eastern Hokkaido, Japan) (Hotes, in press). In an area of ca. 25 ha, reed-sedge vegetation has been replaced by bare peat surfaces, with *Zostera japonica* growing in shallow water. Patches of alder (*Alnus japonica*) trees have equally died. Saltmarsh species (e.g. *Carex subspathacea*, *Potentilla egedei*, *Aster tripolium*, *Puccinellia kurilensis*, *Triglochin maritimum*, *Glaux maritima* etc.) are growing around the dead tree stumps. This vegetation change was detected when series of aerial photographs of Kiritappu Mire taken between 1947 and 1990 were compared. Subsequent investigations on the ground proved that the different colours seen in the photographs indeed were related to changes in plant cover, and that the mud flats are currently expanding upstream.

The water that is supplied to the area through Ichibangawa River has a high electrical conductivity (EC) indicating that the ion concentrations are high (Haraguchi 1995, Saito 1997, Tani 1997). It is probable that an increased influx of sea water is related to the observed vegetation changes. However, reed (*Phragmites australis*) and sedges like *Carex lyngbyei* are known to tolerate high salt contents as well as high water levels, and neither salt stress nor the water level rise alone can explain why most of the area is now bare without any living vegetation. We suggest that the high sulphate concentrations in the floodwater in combination with the wetter conditions are the cause of the reed die-back. Sea water is rich in sulphate, and when this water infiltrates in the soil it becomes anaerobic. Under anaerobic conditions and in the presence of organic material sulphate is reduced to sulphide (S^{2-}) by micro-organisms. Free sulphide is very toxic for higher plant species. In most fens, large quantities of iron (Fe) are present that can bind sulphide in the form of FeS which is harmless to plants. If the iron supply is insufficient, this protective mechanism does not function, and sulphide can accumulate to toxic levels (Smolders and Roelofs 1995). *Phragmites* can protect itself to a certain extent by leaking oxygen from its roots, which oxidises sulphide in the immediate surroundings of the roots. Algal mats on the ground surface can produce oxygen in the toplayer and thus mitigate the effects of sulphide, but only during day time. We put forward the hypothesis that the deep rooting plant species, such as *Phragmites* and *Carex* species suffer from sulphide toxicity during the night. The shallow rooting salt marsh species are not affected or they are better adapted to sulphide stress.

The aim of this research was to clarify the mechanisms of vegetation change along the middle reaches of Ichibangawa River. The hypothesis to be tested is: the vegetation change is caused by high sulphide concentrations in the topsoil formed due to sulphate reduction by micro-organisms under anaerobic conditions.

2. Materials and Methods

2.1. Study area

The study area is located at 145° 3' 00" E, 43° 2' 50" N in the southern part of Kiritappu Mire, near Biwase Village in Hamanaka Town, eastern Hokkaido, Japan (fig. 1). According to the topographical map 1:25,000 the altitude is ca 2.5 m a.s.l., but preliminary ground height measurements by Inoue (unpubl.) suggest that it is probably lower, between 0 m and 0.5 m. The low-lying area extends over ca 1400 m from east to west and over ca 500 m from north to south along the middle reaches of Ichibangawa River. Tidal sea-level changes of the Pacific affect water levels in the study area. The eastern part of the low-lying area is largely free of vegetation. Bare peat surfaces with dead roots and rhizomes of *Phragmites* and *Carex* species are widespread, and large areas are permanently flooded by brackish surfacewater. In these shallow water bodies *Zostera japonica* occurs, but it is rare and its cover is very low. In the western part, saltmarsh vegetation dominated by *Carex subspathacea* is still present but the patches are separated by bare peat surfaces or small water courses. The muddy bottoms of the shallow water tracks often show a greyish or whitish colour indicating the presence of microbial mats. Dead stumps of trees and shrubs are scattered throughout the saltmarsh. The trees are probably alder (*Alnus japonica*) and possibly hydrangeas (*Hydrangea paniculata*) which still can be found in shrub forests along the mire margins outside the area affected by brackish water. *Calamagrostis epigejos* and *Phragmites australis* grow in the slightly elevated patches around the tree stumps together with smaller saltmarsh species.

2.2 Analysis of aerial photographs

A series of aerial photographs taken in 1947, 1975, 1978 and 1990 were used to gain a first overview of how the area affected by vegetation change expanded during 43 years. Structures that were visible in all photographs were used as reference points to plot the movement of the border between affected and unaffected areas between the different years. One useful landmark was a path that was constructed some time between 1947 and 1975 (it is first visible on the 1975 photograph). It starts at the southernmost point of the northern hill and crosses the mire in a straight line towards the south-southeast. A bridge that used to cross Ichibangawa River has collapsed so that only the slightly elevated path with a shallow ditch on either side is left.

As only every second photo of the series was available at Kiritappu Mire Center, no stereoscopic view was possible, and consequently the location of the borders on the map has an estimated error of up to 10 m in the field.

2.3 Water level monitoring, pH and electric conductivity

Two automatic water level recorders were installed by T. Inoue (Laboratory of Land Improvement, Faculty of Agriculture, Hokkaido University) on July 6, 2001. They were placed in Ichibangawa River at a site where an abandoned path which used to cross the mire hits the river course, and on a bare patch between areas with saltmarsh vegetation 80 m north of the river. The water level recorder in the river was a pressure-sensitive type, whereas the recorder in the salt marsh was a float-type. Water levels were recorded every hour and the data stored in a data logger.

In July, pH and electric conductivity were determined in the surface water on bare patches at two sites using a pH/EC meter 24-D of Horiba Ltd.

On July 6 four surface water samples were taken and analysed in the Laboratory of Plant Ecology in Groningen. The samples were taken from surface water in the poor fen, in the reed, in the river and in a ditch which drained water from the mud flats.

2.4. Electrode measurements

In-situ measurements of oxygen saturation, redox potential, and sulphide concentrations were carried out between July 5 and July 7, 2001. The stainless steel needle microelectrodes (van Gemerden 1993) were attached to a micro-manipulator that allowed to measure profiles with a maximal resolution of 0,01 mm and a maximal depth of 25 cm. This equipment was originally developed in microbiology for ecological research of marine mudflats (de Wit et al. 1989; Visscher et al. 1991) but can be used also in freshwater systems such as poor fens and dune slacks (Grootjans et al 1997, Adema et al. 2002). Vertical profile measurements were conducted on July 6 between 10:30 and 13:00 in four sites: Bare peat 1, bare peat 2, *Carex* and *Phragmites*. Two electrodes for each of the three parameters (oxygen saturation, redox potential, sulphide concentration) were attached to the micro-manipulator, and their respective values were measured between 0 mm and 250 mm depth. Between 0 and 10 mm the electrode tips were lowered in 0.5 mm steps, between 10 mm and 25 mm in 1 mm steps, between 25 and 50 in 5 mm steps, and between 50 mm and 250 mm in 10 mm steps.

Temporal changes during a day/night/day period were measured on a bare patch between 16:20 on July 5 and 10:00 on July 6. The same time series measurements were repeated on a site with *Phragmites* at the margin of the area affected by brackish water between 13:20 on July 6 and 10:00 on July 7. All data were stored in a data logger.

2.5. Vegetation survey

A transect survey of the vegetation was conducted on September 10, 2001, along a line reaching from Ichibangawa River in the south to the foot of the hill in the north, after preliminary investigations on June 25 and July 5-7. The transect was situated ca 25 m east of the abandoned path crossing the mire in south-southeastern direction. Only the horizontal distribution of plant species along the transect was recorded as well as the overall height of each species in each section. More detailed surveys with estimation of the density and cover were prevented by rain and strong wind.

3. Results

3.1 Aerial photographs

The expansion of the area affected by vegetation die-back between 1947 and 1990 is shown in figure 2. On the black and white aerial photographs, water appeared dark grey to black (unless it reflected direct sunlight in which case it could appear white). The bare peat surface was reproduced in dark grey, though generally in a lighter colour than open water. Alder forest was medium grey, whereas mostly herbaceous mire vegetation appeared in different shades of light grey. Based on these observations, the border between the area covered predominantly by living vegetation and the area where bare peat or water were exposed was drawn for each of the four years for which aerial photographs were available. In 1947 bare surfaces were restricted to a belt ca 30-50 m wide along the river. In 1975 the picture had changed considerably since the zone nearly devoid of vegetation had expanded to a line ca 200 m north of the river and ca 50 m to the south. This bare area had also expanded ca. 200 m upstream. In the three years till 1978 there was a further increase in bare area by 50-100 m towards the west. This tendency continued during the next twelve years, and the western border moved 150-200 m westwards. A slight expansion was also found at the margins of the bare area in the north, east and south. In 2001, the brackish water influence had reached the transect of the vegetation survey and even to the west of the abandoned path through the mire. Bare patches with remains of dead reed and sedges could be seen in this part of the mire, too.

3.2. Water level monitoring, pH and surface water composition

The water levels of Ichibangawa River and on the adjacent mudflat showed the influence of tidal cycles (fig. 3). The influence of rainfall on water levels was not pronounced; the effects of the tides were clearly predominant. A 12-hours-cycle as well as a 14-days-cycle, caused by the cyclic shifts of the lunar phase were reflected in the data. It is

noteworthy that the peaks of the 12-hours cycle rhythmically went through phases in which the first and the second daily maximum differed strongly. The difference gradually became smaller till both daily peaks were about the same, and then the peak which was more pronounced before gradually diminished while the other one increased until the cycle began again. These shifts seem to be due to interference of the two lunar cycles, although the actual water levels in the river were probably altered by the local weather conditions.

The amplitude of tidal fluctuations in Ichibangawa River reached up to 60 cm, whereas on the bare patch in the saltmarsh area it did not exceed 45 cm. In general, the curves for both sites fluctuated synchronously, but the water level in the saltmarsh mostly dropped only to a level of about 10cm approximate ground height and did not fall further even when the river water level continued to drop. In some cases the recorder showed no increase in water level although the site should have been flooded according to the level of the river. The small pit that had been dug for the float quickly silted up with fine mud, preventing the float from dropping further even if the water level did drop below the surface level, and adhesive forces obviously kept the float down in cases where there was only a small water level rise.

According to the ground height measurements of T. Inoue (fig. 4), the whole area along the south-north transect is flooded up to a point 150 m north of the river at least every two weeks.

The two in-situ measurements of pH and electric conductivity in surface water yielded similar results (table 1). Both pH values were between 7 and 8, and the electric conductivity was about 32000 $\mu\text{S}/\text{cm}$. Measurements of the pH in the uppermost 5 cm of the soil showed lower values than the surface water (5.9 – 6.4). There were no differences in pore water pH between bare patches and stands of *Carex subspathacea*.

The analysis of the surfacewater in the laboratory at Groningen University showed that the water in the river and in the reed zone had the lowest concentrations of dissolved minerals, although the sulphate and chloride concentrations were still high. The pore water was very low in dissolved minerals and the pH was also low (4.7). The surface water samples in a ditch that drained the mudflat showed very high values of sulphate and chloride, much higher than in the river at the site of the collapsed bridge. The highest iron concentrations were found in the surfacewater of the reed zone.

3.3. Electrode measurements

The profile measurements showed differences in oxygen saturation, redox potential and sulphide concentration between the bare patches, the *Carex* stand and the *Phragmites* stand (fig. 5 a-c).

Super-saturation of oxygen up to 180 % was measured in the uppermost 3.5 mm of the bare peat site and 8 mm of the *Phragmites* site. Such high values were not detected in the *Carex* stand where the oxygen was immediately depleted to very low levels. Below 8 mm depth no significant oxygen levels were detected at the *Carex* site and the *Phragmites* site as well. Only one electrode at the *Phragmites* site, measured super-saturation of oxygen at 150 mm depth.

Redox potentials generally were negative and dropped with increasing depth. The only exceptions were electrode a at the bare peat site 1 and the *Phragmites* site. At the former, -4.6 mV were measured at 0 mm and 1.2 mV at 100 mm, but from there on the values dropped again to -19.1 at 250 mm depth. At the *Phragmites* site, electrode a measured a steep increase in redox potential from -99.9 mV to -78.7 mV in the uppermost 50 mm, and a slower increase to -71.9 mV at 250 mm depth. The lowest redox potentials were measured at the *Carex* site where both electrodes gave similar results. A steep decrease from -68.1 mV to -113.0 mV (electrode a) and from -24.4 mV to -130.4 mV (electrode b) occurred over the first 50 mm. Below that depth, the values continued to drop to -199.1 mV and -175.9 mV, respectively, at 250 mm depth.

Sulphide concentrations showed the greatest differences between the sites among the measured parameters. Electrode a yielded zero values for all depths at all sites, so that only the values of electrode b could be used. Sulphide concentrations stayed low (3-6 $\mu\text{mol/l}$) to 120 mm depth and then increased gradually to 57 $\mu\text{mol/l}$ at 250 mm depth at the site bare peat 1. At bare peat site 2, a faster increase from 0 $\mu\text{mol/l}$ at the surface to 102 $\mu\text{mol/l}$ at 160 mm depth was found, and below that a sudden increase to 339 $\mu\text{mol/l}$ at 190 mm depth occurred. From there on the values dropped slightly to 320 $\mu\text{mol/l}$ at 250 mm depth. At the *Carex* site, values between 12 and 17 $\mu\text{mol/l}$ were measured from 0 to 100 mm depth; the electrode failed between 110 and 150 mm, and between 160 and 250 mm a further increase of the sulphide concentration from 104 to 226 $\mu\text{mol/l}$ was detected. At the *Phragmites* site, the sulphide concentration increased only slightly from 1 to 4 $\mu\text{mol/l}$ over the whole profile.

The time series measurements in a bare patch yielded reliable results only between 6.00 and 10.00 in the morning (fig.6 a). During the rest of the night the electrodes did not respond due to heavy rain. The sulphide concentrations (at 50mm below the surface) were very high and ranged between 700 and 800 $\mu\text{mol/l}$. The redox potential was also

low (between -120 and -150mV). In the *Phragmites* stand only one sulphide electrode functioned properly during the night (fig. 6 b). The measurements showed that the sulphide concentrations increased during nightfall and remained high (between 200 and 350 mV) until the measurements were stopped the next day at 10.30 in the morning.

The redox potentials were between 0 and -120mV . The values of around 0 originated from one electrode, which might not have functioned well or was measuring inside or close to a *Phragmites* root.

The oxygen values were close to zero during the whole night.

3.4. Vegetation survey

26 plant species were found along the transect between Ichibangawa River and the foot of the hill (table 2). In addition to the species given in table 2, *Carex mackenziei*, *Scirpus cf. tabernaemontani* and *Zostera japonica* were also found in the area. In the section of the transect between 0 m (river bank) and 119 m salt marsh plants were dominant. These were generally less than 50 cm high. Only a few scattered individuals of *Phragmites australis* (120 cm) and *Calamagrostis epigejos* (130 cm) stood out from the low vegetation. A transitional zone from 119 m to 136 m lacked most of the typical salt marsh species as well as the species growing in the higher parts of the transect. *Calamagrostis epigejos* and *Phragmites australis* formed denser stands here than in the section closer to the river and reached 140 cm and 170 cm , respectively. The area between 136 and 156 m contained mostly species that were not found closer to the river. However, elements of the salt marsh vegetation (*Stellaria humifusa*) and of reed beds with brackish water influence (*Rubia yezoensis*) occurred up to 142 m . *Phragmites australis* was found up to the end point of the transect at 156 m .

Figure 7 shows the distribution of 10 selected plant species along the transect and the location of bare areas. *Carex subspathacea* is abundant in the lowest part where it forms monodominant stands. In a few sites between 70 and 90 m *Eleocharis kamtschatica* is mixed with this species, and *Triglochin palustre* (frequent) and *T. maritimum* (rare) as well as *Potentilla egedei*, *Carex lyngbyei*, *Aster tripolium*, *Glaux maritima* and *Carex mackenziei* (the latter three not shown) were equally found in the low (less than 50 cm) saltmarsh vegetation. *Stellaria humifusa* occurred here, too, but this species reached further into the higher vegetation dominated by *Phragmites* and *Calamagrostis* and thus differed from the above-mentioned. All species apart from *Carex subspathacea* and *Eleocharis kamtschatica* were absent from the lowest sections of the transect with ground heights between 0 and 0.1 m . The restriction to higher sites with at least 0.2 m ground height was obvious for *Sonchus brachyotus*, *Calamagrostis epigeios* and *Phragmites australis*. *Calamagrostis langsdorffi* occurred only where the ground was more than 0.3 m approximate height; the two *Calamagrostis* species were mutually

exclusive along the transect. All other species listed in table 2 were found only above 0.4 m.

4. Discussion

The area in which the drastic vegetation shifts have occurred since 1947 is particularly low-lying. Although the ground height measurements are only approximations due to lack of accurate benchmarks in the vicinity, it is probable that its surface is less than 0.5 m a.s.l. This area can be distinguished from the adjacent higher mire area already on the 1947 aerial photograph due to its lighter colour, and because patches of dark alder stands line the border between the lower and higher parts of the mire. In the 28 years between 1947 and 1975, the eastern part of the area lost almost all living vegetation. It seems to be permanently covered by water now, although long-term measurements of water levels are not available. Open water is indicated for this location on the topographical maps 1:50000 (revised 1983) and 1:25000 (revised 1991). Since 1975 the expansion of the affected area has been mostly in western direction. In the north, east and south the shallow basin is bordered by elevated areas that prevent further spreading of brackish water. The speed is considerable with 50-100 m in three years between 1975 and 1978, and 150-200 m in twelve years between 1978 and 1990. The expansion in the eleven years till 2001 seems to have slowed down and lies in the range of 10-20 m. From these observations it can be concluded that a relative increase in water level has taken place, and the fact that the area affected by vegetation change has kept expanding to the present day suggests that the water level is still rising now. This leads to the question of what causes the rise. Theoretically, three different causes can be distinguished:

- (i) As the Pacific coast of eastern Hokkaido is located at the Kuril subduction zone, subsidence of the earth's crust seems a possible factor. Okazaki (1986) postulates such a subsidence for Kiritappu Mire.
- (ii) Secondly, a rise of the sea-level might be occurring that brings more water into the river systems of the mire. The influence of Holocene sea-level changes on coastal aquatic ecosystems in eastern Hokkaido is documented in the literature (Ohira 1994, Sawai and Kashima 1996). With the current tendency towards higher mean temperatures world wide, melting of the polar ice caps is increasing and this is expected to lead to rising sea-levels.
- (iii) Third, changes of the river morphology might have caused or contributed to the increased saltwater influx. The common mouth of Ichibangawa River, Nibangawa River, Biwase River and Dorogawa River has been changed into a fishing port with vertical concrete piers on both banks. The construction work was carried out in several steps as can be seen on the series of aerial photographs, so that a

gradually increasing influence of the changed morphology on the river water levels might be possible.

In a preliminary survey of the stratigraphy in the area, S. Hotes found peat depths of 60 cm overlying sand and a tephra layer in 40 – 45 cm depth at a site 1 m north of the Ichibangawa River. The peat consisted predominantly of sedge and reed roots and rhizomes. This indicates freshwater conditions for several centuries during which the peat layer could accumulate.

The water level changes of Ichibangawa River are clearly influenced by tidal fluctuations of the sea-level. The maximum amplitude of 0.74 m is similar to that measured at Kotoiso Bridge in Biwasegawa River (Hotes et al. 2001). The water level data for the shallow water track in the salt marsh correspond well with those of the river, but some inaccuracies may have been caused by the fragile mechanics of the float that make this type of water level recorder less suitable for the location.

The maximum water level in the salt marsh is 1.8 cm higher than in the river. If this difference is not due to a measurement error, it could have been caused by differential movement of the water in the water tracks through which the tidal water is supplied to and drained from the salt marsh. Easterly winds might also have blown water over the mudflat towards its western margin, thus causing the slightly higher level.

Electric conductivity and pH of the surface water in the salt marsh showed high values only slightly lower than those of the Pacific seawater (Saito et al. 1997), indicating that the water in the river is mostly supplied from the sea and to lesser extent from the catchment area. This finding was supported by the analyses of the surfacewater samples showing very high chloride, sodium and sulphate values in the water leaving the mudflats through the ditch along the abandoned path. Ichibangawa River itself had considerably lower pH, EC and ion concentrations than the water in the mudflat. Thus it can be concluded that the brackish water supplied to the mudflat enters the area at a point further downstream where the influence of seawater is stronger, and part of this salt-rich water flows back into the river at low tide through the ditch. In the river it is diluted by freshwater that is supplied from the catchment area.

Changes of the oxygen saturation, redox potential and sulphide concentration with the depth showed differences between the bare patches, the *Carex* stand and the *Phragmites* stand. The pattern for oxygen saturation shows a thin hypersaturated surface layer, below which oxygen is quickly depleted. The hypersaturation is probably caused by photosynthetic activity of micro-organisms in the top layer (van Gernerden 1993). The lack of such an enriched layer in the *Carex* stand might indicate that such

microbes were not present at the locations where the electrodes were inserted. The high oxygen saturation in 150 mm depth at the *Phragmites* site perhaps was caused by oxygen leaking from a plant root.

The results gained for the redox potential do not fully meet the expectations based on the hypothesis that the bare patches should show the lowest, the *Carex* stand medium, and the *Phragmites* stand the highest values. When considering only the curves for *Phragmites* b, bare peat 1 b and bare peat 2 a + b, the expected relation is found, but the *Carex* stand shows the lowest of all values and the fastest decrease with increasing depth. This, however, fits well with the zero oxygen saturation at this site through the whole profile. The increasing redox potential measured with electrode bare peat 1 and *Phragmites* are difficult to interpret. If they were not caused by technical problems of the equipment, supply of oxidative substances to the deeper layers must have taken place.

The sulphide electrode failed and therefore only one curve for each location could be gained, but these exhibit the expected pattern. High concentrations were found in the bare patches, medium values in the *Carex* stand, and very low values in the *Phragmites* stand. The difference in sulphide concentrations between bare peat 1 and bare peat 2 corresponds with the differences in redox potential: bare peat 1 had a higher redox potential than bare peat 2, and the sulphide concentrations show a reciprocal pattern. Sulphide production can take place in a redox potential range between 0 and -150 mV (Sikora and Keeney 1983) so that sulphide could be present at all depth when judging based on the measured redox potentials. However, sulphide production depends on more factors than just the redox potential (van Gemerden 1993) which explains why the sulphide concentrations do not follow the changes in redox potential that closely.

The time series measurements during the night at 50 mm below the surface yielded very interesting results, although the electrodes failed in the bare peat stand during most of the night. The expected increase of sulphide concentrations during the night could be shown for the *Phragmites* site, and the very high concentration at the bare site backs the hypothesis that sulphide toxicity is the reason for the observed vegetation change. For some aquatic macrophytes such as *Stratiotes aloides* and *Potamogeton compressus*, sulphide concentrations as low as 10 $\mu\text{mol/l}$ can be toxic (Smolders and Roelofs 1995). The values which were detected during the profile measurements at the bare peat sites and the *Carex* site are up to 34 times higher than this. The still higher sulphide concentrations (more than 600 $\mu\text{mol/l}$) from the time series measurements in the bare soil exceed the tolerance threshold of *Phragmites australis* (500 $\mu\text{mol/l}$). In the reed zone the values were much lower (300 $\mu\text{mol/l}$). The fact that *Phragmites* in this zone was still very viable indicates that most of the sulphide produced was fixed, probably by iron. This supply of iron originates from the poor fen. *Phragmites* is situated here in the seepage

zone of the poor fen, which can clearly be seen from the bacterial film on the surface water. This bacterial film consists of iron reducing bacteria and the presence of these “oily” films generally indicates the presence of iron-rich water.

The vegetation survey was carried out in an area where changes have begun probably in the 1980s. Relatively high plant cover rates were recorded in 2001, and formation of patches devoid of vegetation has only started in the lowest lying sections. Even here, alder (probably *Alnus japonica*), that on the 1947 aerial photograph seems to be well developed, has died completely. *Phragmites australis* as well as the relatively salt-tolerant *Carex lyngbyei* (which together probably dominated the vegetation 50 years ago), are left only in the highest areas. These species occur widely in coastal wetlands in the northern hemisphere (Dierssen 1996), and it is unlikely that increased salinity and higher water levels can be the proximate factors which lead to their local extinction. The results of our investigations suggest that supply of sulphate-rich water to a site with anaerobic substrate conditions and small sulphide binding capacities due to a lack of iron has led to accumulation of sulphide up to concentrations that are toxic for macrophytes. Deep-rooting plants like *Phragmites* or *Magnocarices* suffer first from this and are replaced by highly salt-tolerant species with shallow root systems. If water levels continue to rise and sulphide concentrations rise also in the upper substrate layer, these species also die and leave bare peat surfaces are inhabited only by micro-organisms.

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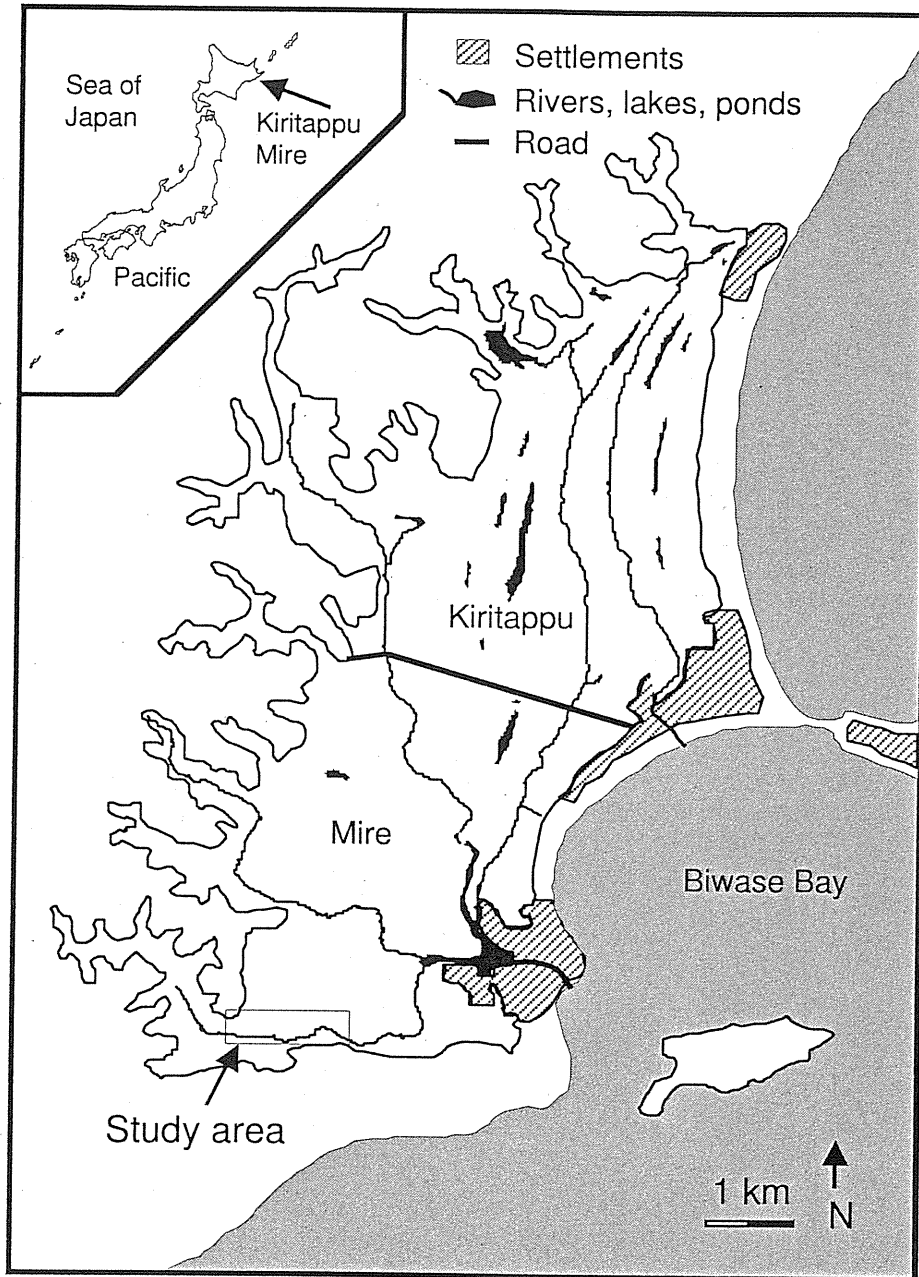


Fig. 1 Location of the study area

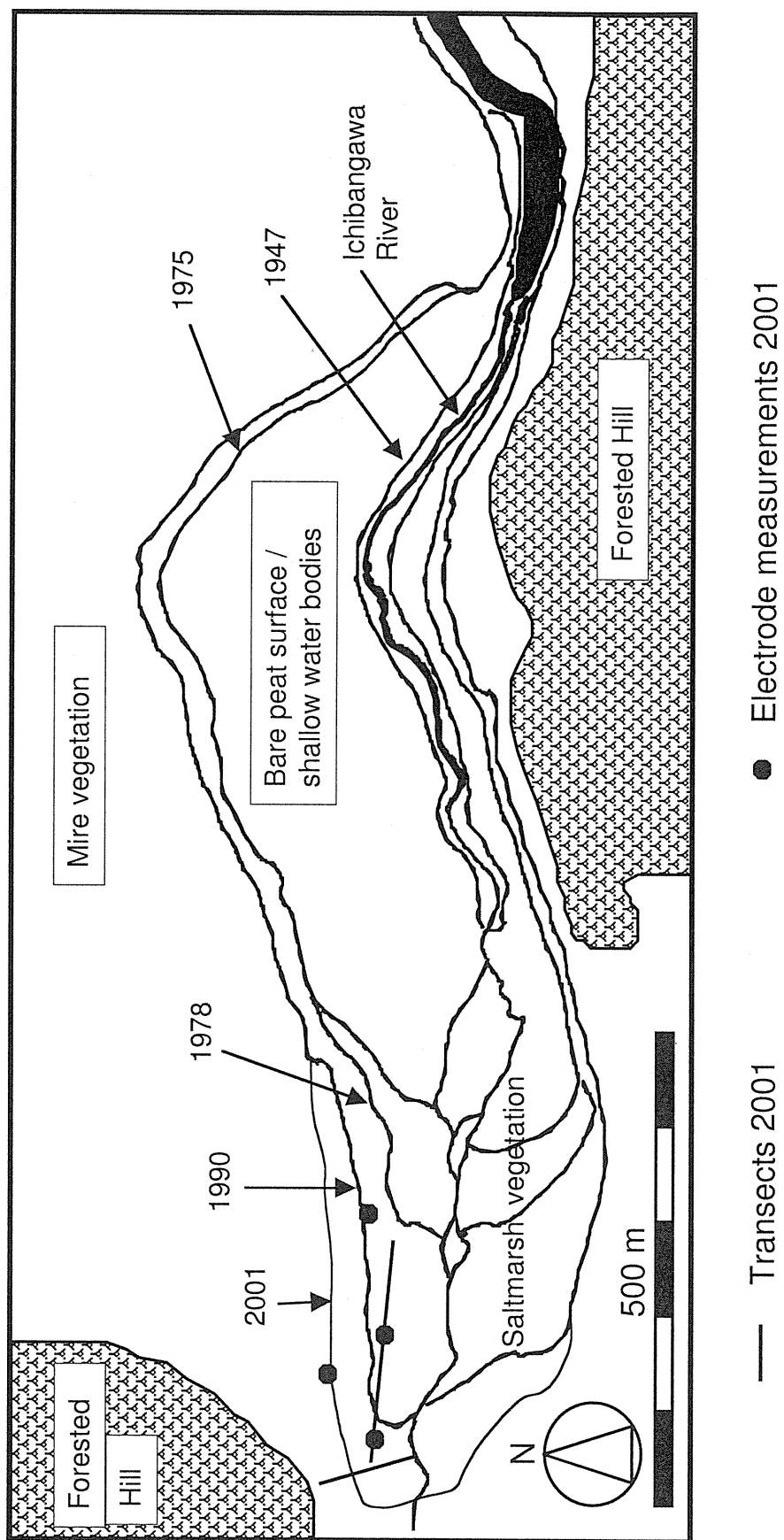


Fig. 2 Expansion of the area affected by vegetation change

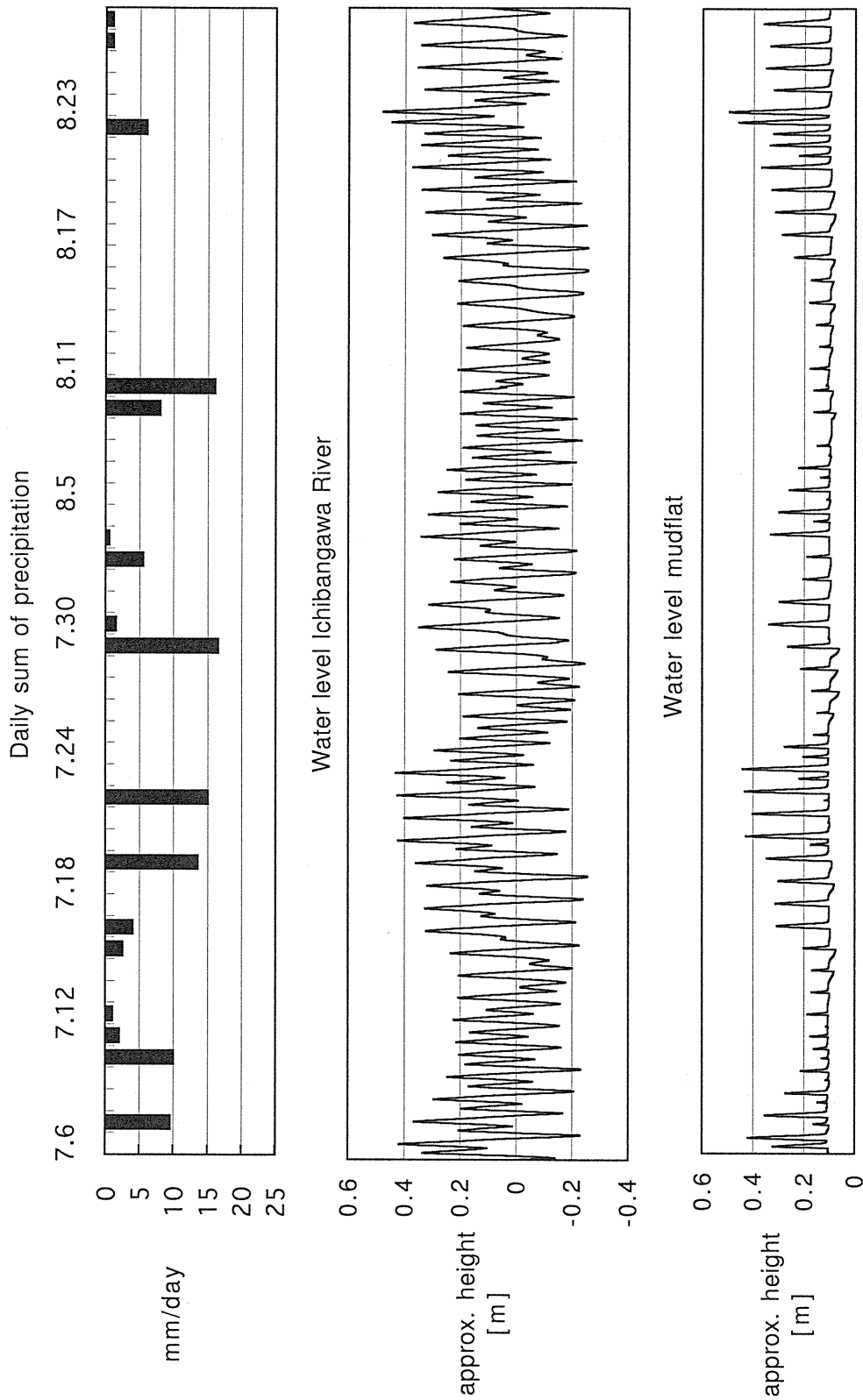


Fig. 3 Daily sum of precipitation, water level fluctuations of Ichibangawa River and water level fluctuations on the mudflat between July 6 and August 28, 2001

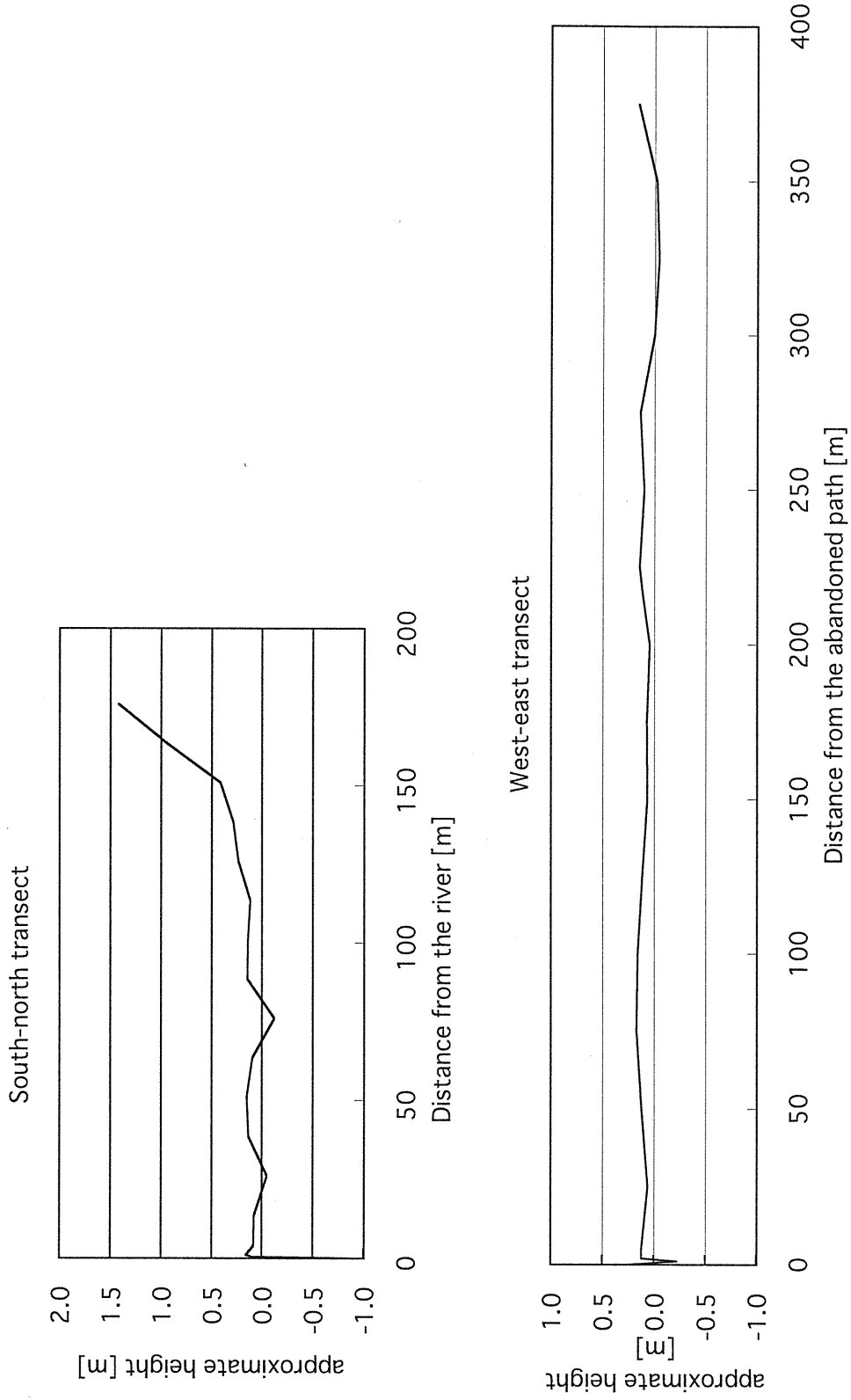


Fig. 4 Ground heights along the south-north transect (from Ichibangawa River to the foot of the hill) and the west-east transect (parallel to Ichibangawa River, through the "bare peat" measurement sites)

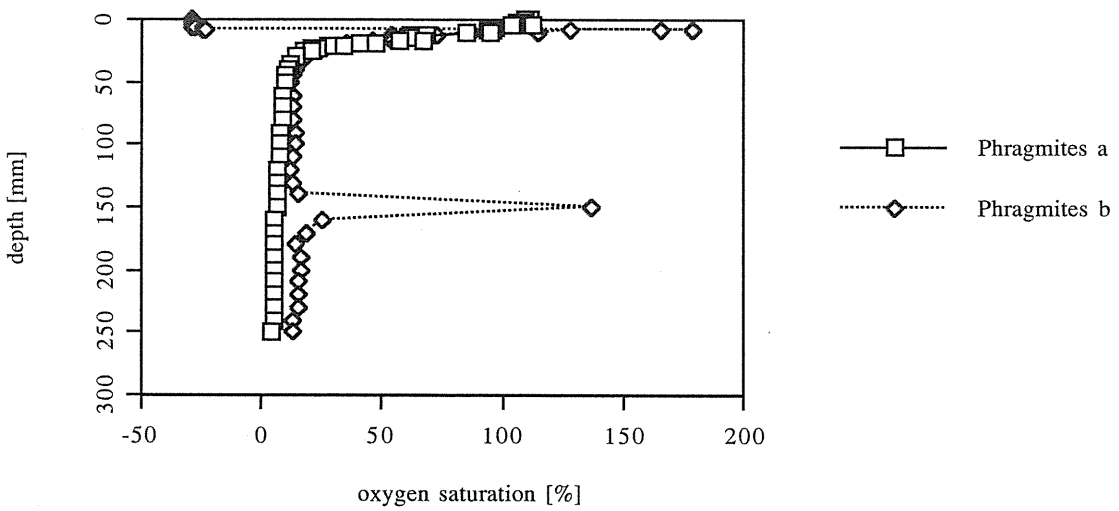
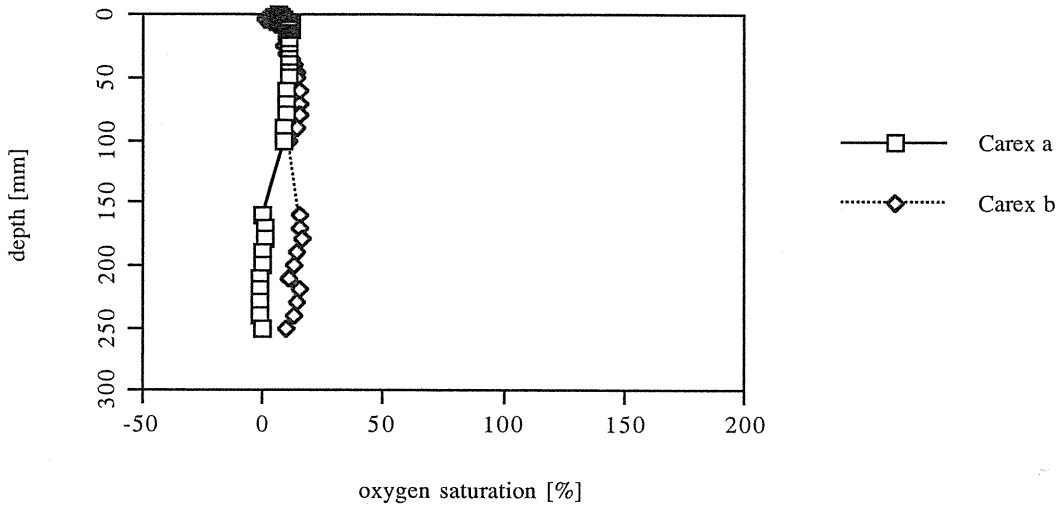
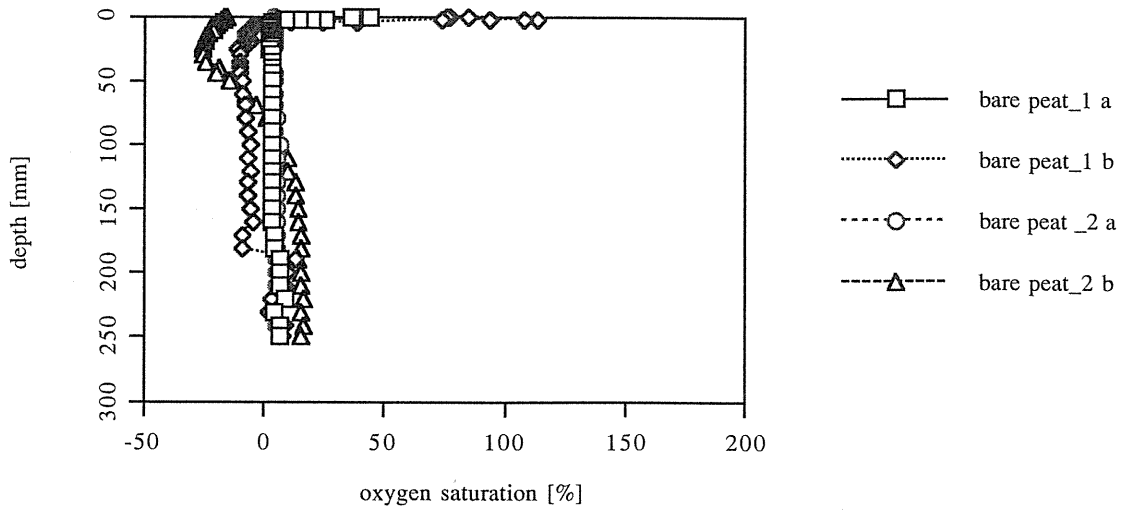


Fig. 5.a) Profile measurements of oxygen saturation at four sites (bare peat 1 and 2; *Carex*; *Phragmites*)

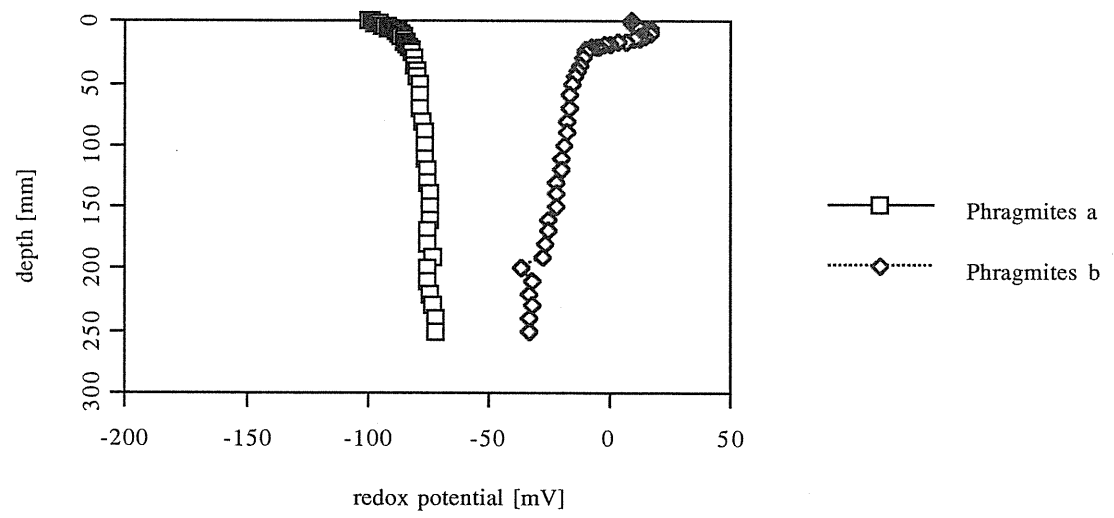
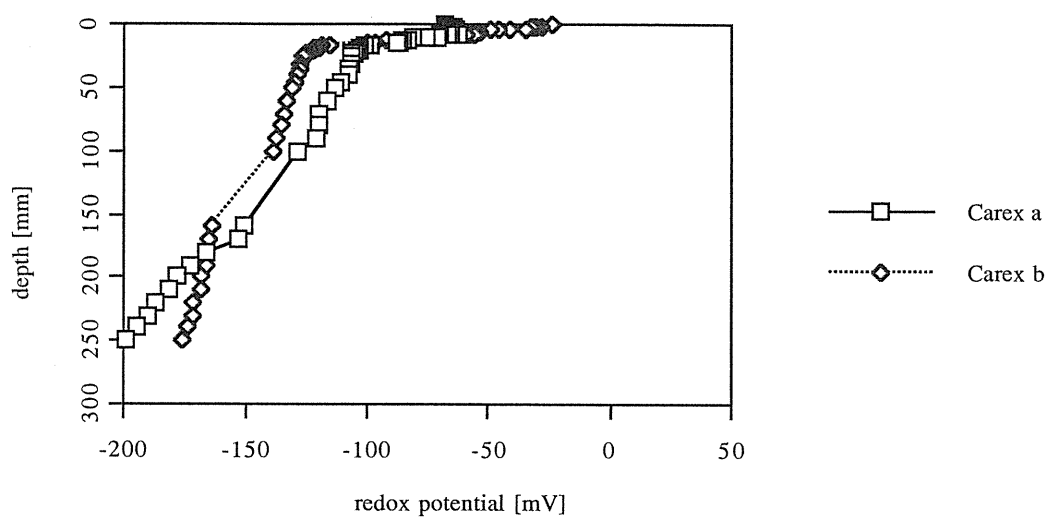
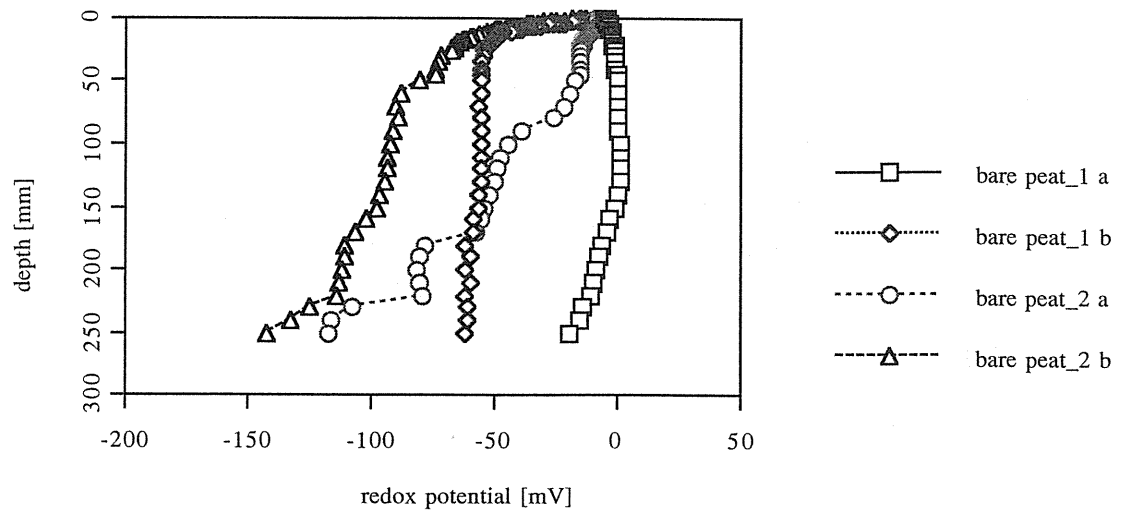


Fig. 5.b) Profile measurements of redox potentials at four sites (bare peat 1 and 2; *Carex*; *Phragmites*)

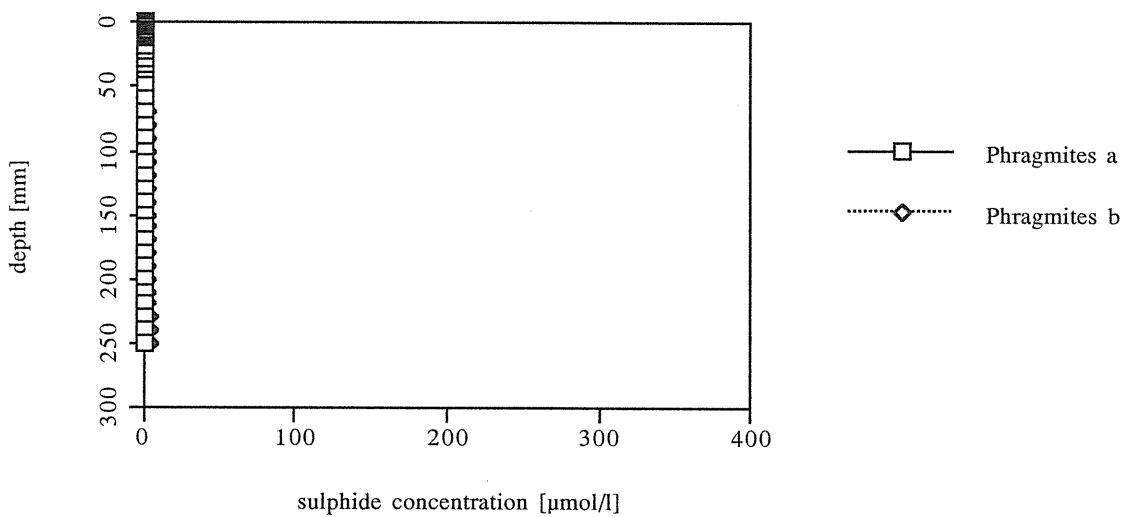
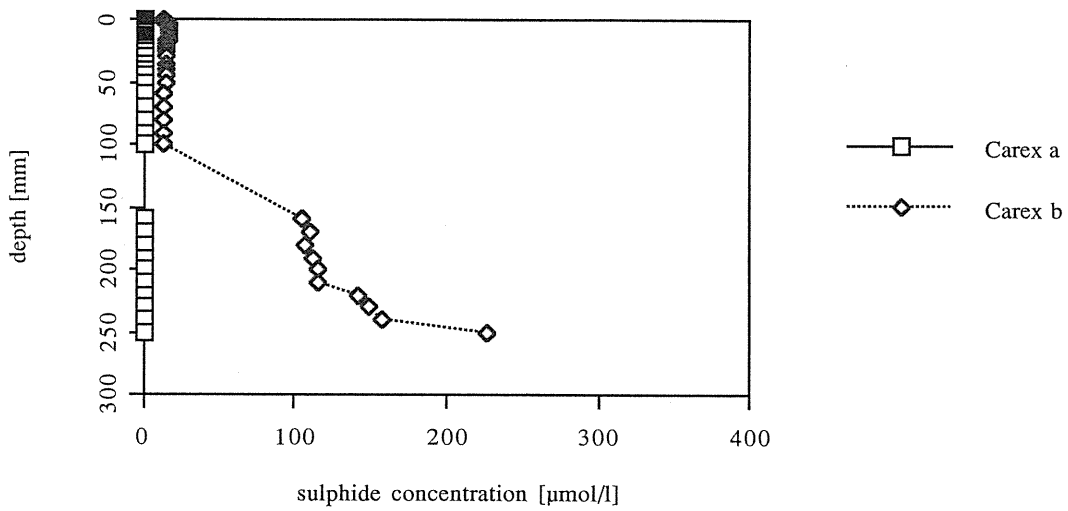
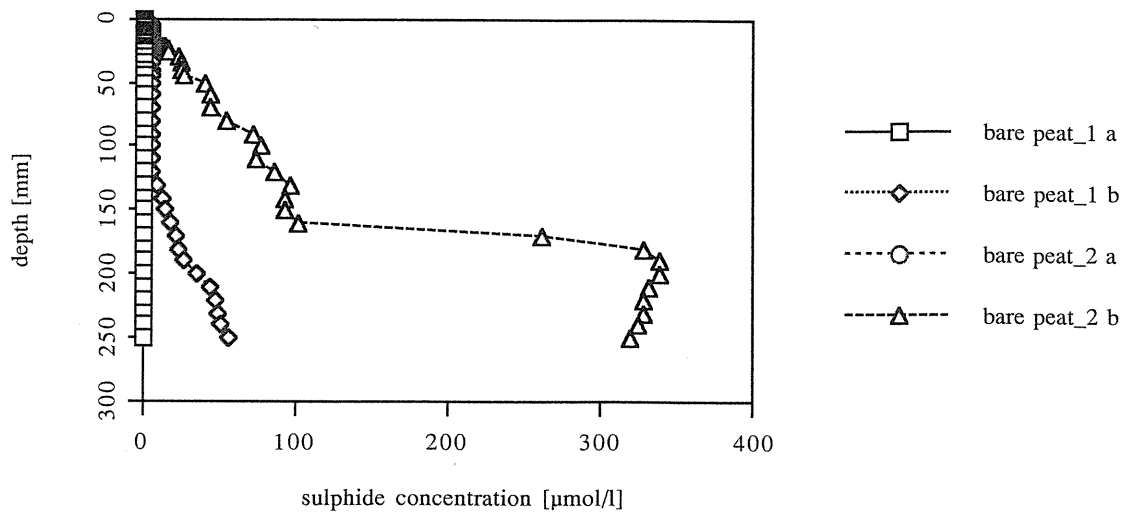


Fig. 5.c) Profile measurements of sulphide concentrations at four sites (bare peat1 and 2; *Carex*; *Phragmites*)

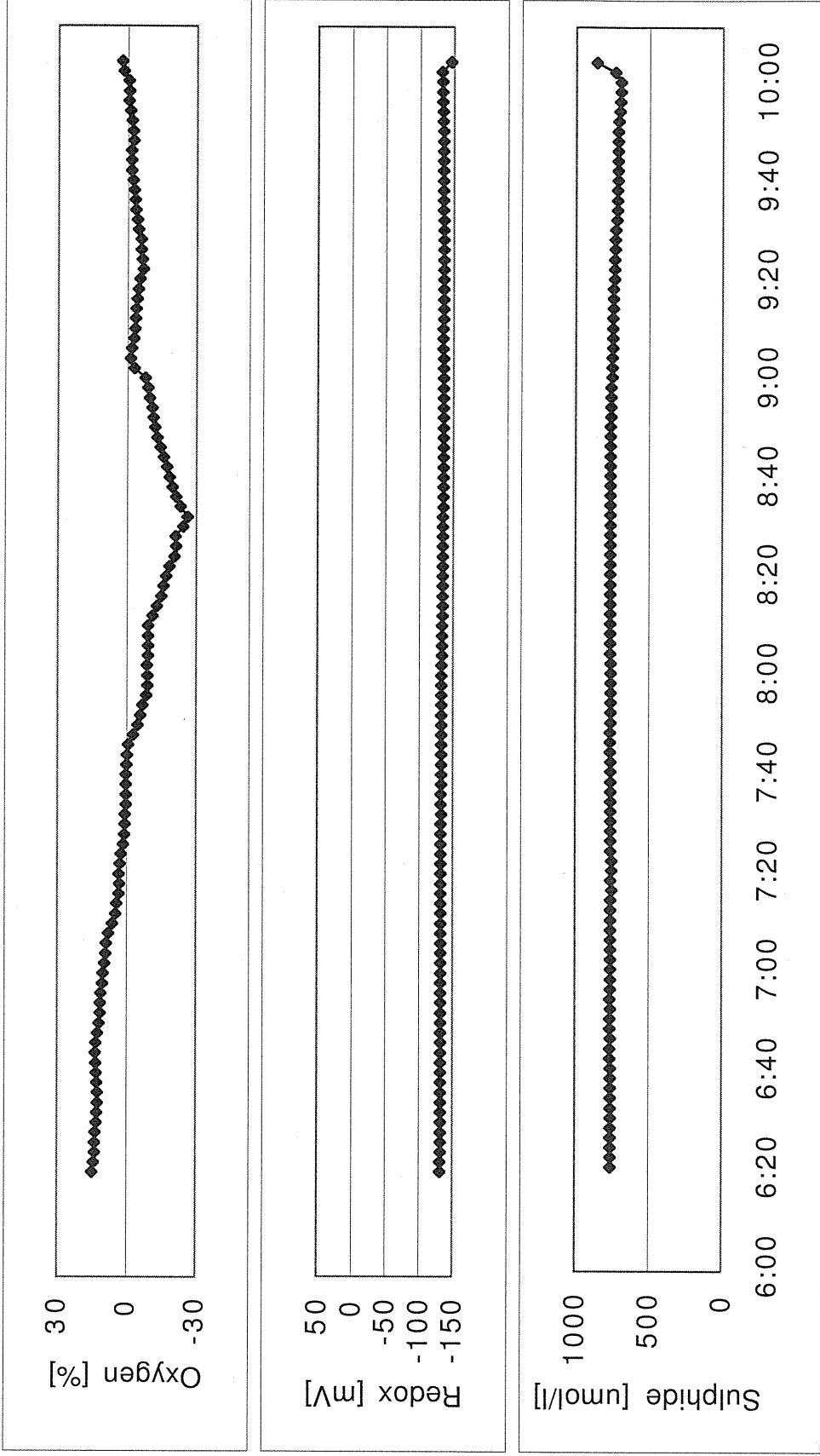


Fig. 6.a) Time series measurements of oxygen saturation, redox potential and sulphide concentration at 30 mm depth in a bare peat patch on July 6, 2001, between 6:00 and 10:00.

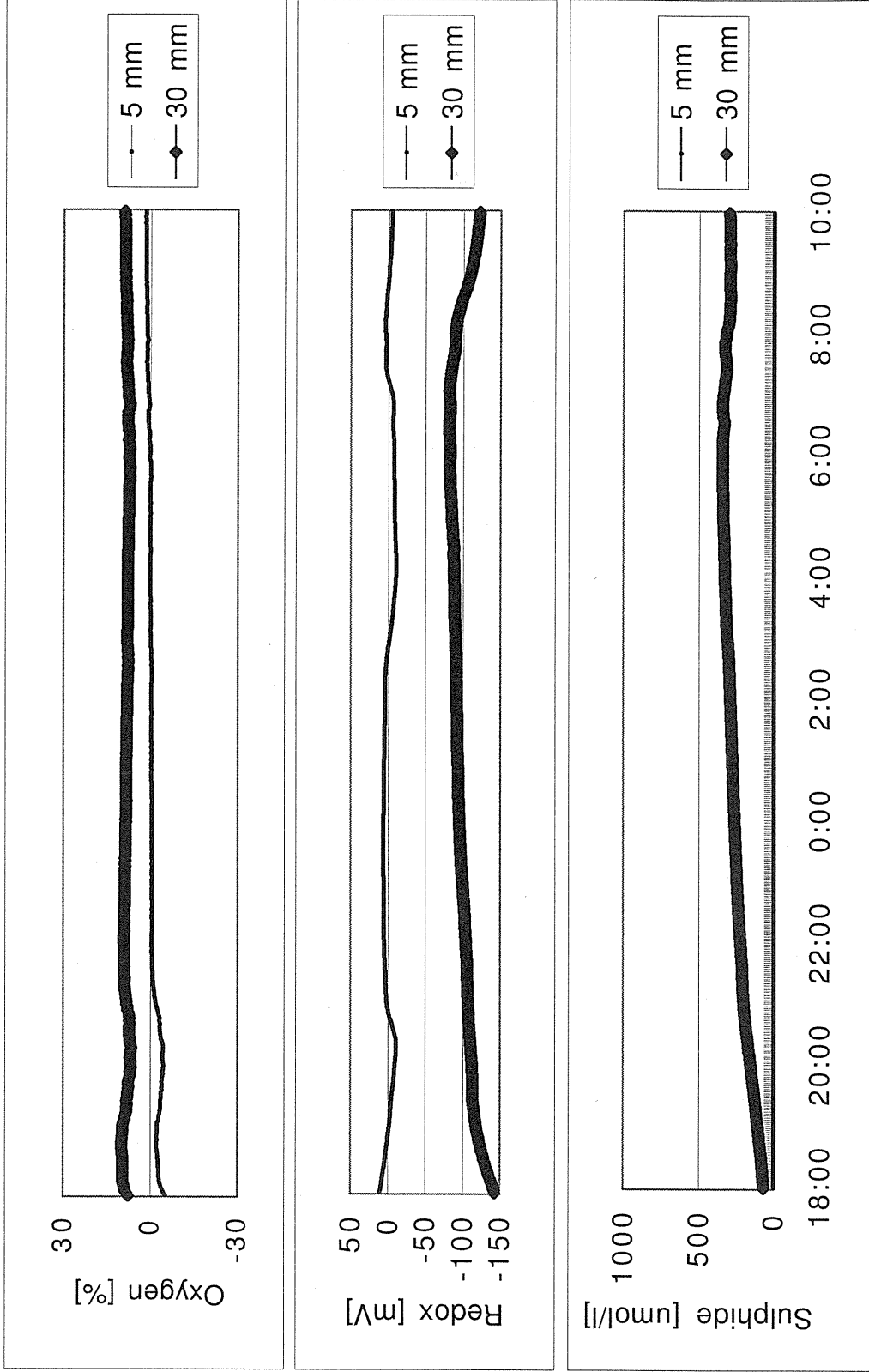


Fig. 6.b) Time series measurements of oxygen saturation, redox potential and sulphide concentration at 5 mm and 30 mm depth in a *Phragmites* stand on July 6/7, 2001, between 18:00 and 10:00.

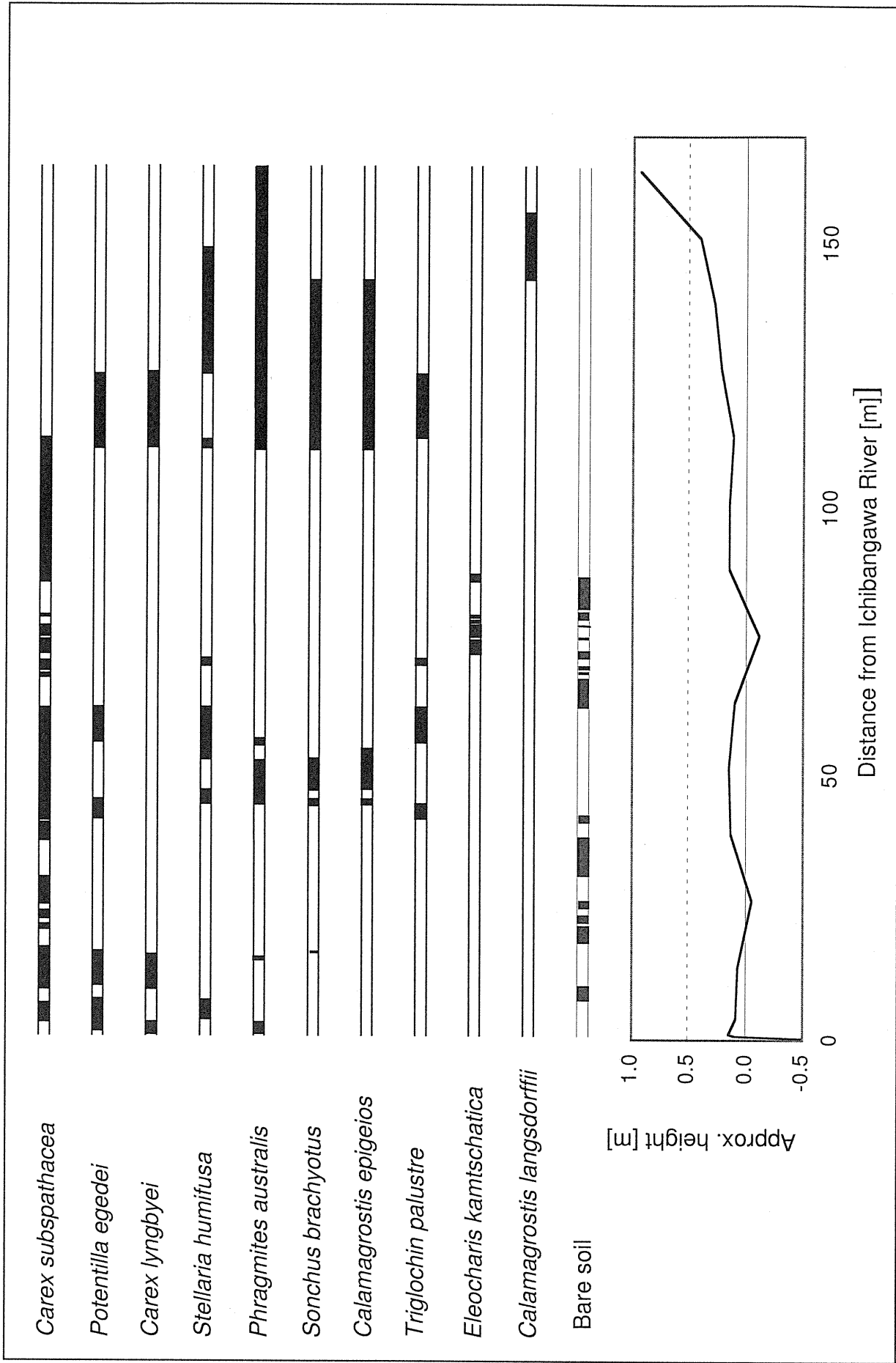


Fig. 7 Distribution of selected plant species along the south-north transect

Table 1 Chemical characteristics of water at the middle reaches of Ichibangawa River

Sampling date	EC μS/cm	pH	CO ₂ mg/l	HCO ₃ ⁻ mg/l	Cl ⁻ mg/l	SO ₄ ⁻ mg/l	Na ⁺ mg/l	K ⁺ mg/l	Mg ²⁺ mg/l	Fe ³⁺ mg/l	PO ₄ ³⁻ mg/l
Surface water, in-situ measurement											
Mudflat west	05.07.2001	32800	7.01								
Mudflat east	06.07.2001	31500	7.73								
Pore water of soil in 5 cm depth, in-situ measurement											
Bare peat	06.07.2001		6.4								
Bare peat	06.07.2001		6.3								
Bare peat	06.07.2001		6.4								
<i>Carex subspathacea</i>	06.07.2001		5.9								
<i>Carex subspathacea</i>	06.07.2001		6.2								
<i>Carex subspathacea</i>	06.07.2001		6.1								
Surface water, laboratory measurement											
Poor fen	06.07.2001	37.6	4.7	20.33	0.49	6.60	9.39	3.73	0.06	0.71	1.07
Reed	06.07.2001	8940	4.5	96.10	0.00	2500.00	255.00	1641.72	61.20	158.22	29.95
River	06.07.2001	8210	6	17.42	31.35	2250.00	248.00	1332.41	56.51	158.37	0.80
Ditch	06.07.2001	32700	7.1	15.84	107.85	11617.00	1480.00	8933.79	259.02	710.14	0.83
Reference data for Ichibangawa River from earlier reports											
Tani et al. 1997		2745	5.95		17.75	393.53	103.71	197.17	9.70	56.40	0.44
Saito et al. 1997		573	6.3				75.60	6.90			0.01

Table 2 Plant species along the south-north transect

No.	Species name
1	<i>Alnus sp.</i>
2	<i>Aster tripolium</i>
3	<i>Calamagrostis epigejos</i>
4	<i>Calamagrostis langsdorffi</i>
5	<i>Carex lyngbyei</i>
6	<i>Carex subspathacea</i>
7	<i>Eleocharis kamtschatica</i>
8	<i>Equisetum palustre</i>
9	<i>Glaux maritima</i>
10	<i>Impatiens noli-tangere</i>
11	<i>Lysimachia thyrsoflora</i>
12	<i>Osmunda cinnamomea</i>
13	<i>Phragmites australis</i>
14	<i>Polygonum sieboldii</i>
15	<i>Polygonum thunbergii</i>
16	<i>Potentilla egedei</i>
17	<i>Puccinellia kurilensis</i>
18	<i>Rubia yezoensis</i>
19	<i>Scutellaria strigillosa</i>
20	<i>Solanum megacarpum</i>
21	<i>Sonchus brachyotus</i>
22	<i>Spiraea salicifolia</i>
23	<i>Stellaria cf. palustre</i>
24	<i>Stellaria humifusa</i>
25	<i>Triglochin maritimum</i>
26	<i>Triglochin palustre</i>