Nutrient retention in a restored peatland buffer

NIKO SILVAN

ACADEMIC DISSERTATION

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Työn ohjaajat / *Supervisors*

Docent Jukka Laine, Department of Forest Ecology, University of Helsinki, Helsinki, Finland
and
Docent Harri Vasander, Department of Forest Ecology, University of Helsinki, Helsinki, Finland.

Esitarkastajat / *Reviewers*

Ph.D. Mika Nieminen, the Finnish Forest Research Institute, Vantaa Research Centre, Vantaa, Finland
and
Prof. Ülo Mander, Department of Physical Geography and Landscape Ecology, University of Tartu, Tartu, Estonia.

Vastaväittäjä / *Opponent*

Prof. Leena Finér, Faculty of Forestry, University of Joensuu, Joensuu, Finland.

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II. Silvan, N., Regina, K., Kitunen, V., Vasander, H. & Laine, J. 2002. Gaseous nitrogen loss from a restored peatland buffer zone. Soil Biology and Biochemistry 34: 721-728.

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IV. Silvan, N., Tuittila E.-S., Kitunen, V., Vasander, H. & Laine, J. 2004. Nitrate uptake by *Eriophorum vaginatum* controls N_2O production in a restored peatland [submitted to Soil Biology and Biochemistry].

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Author's contribution

Papers **I−V**: Niko Silvan was responsible for theoretical and practical planning of the substudies, carrying out the field works, performing statistical analyses, interpreting the results, writing the first versions of the manuscripts and the preparation of the manuscripts at the final stages. Jukka Laine and Harri Vasander participated in theoretical and practical planning of the substudies and preparation of the manuscripts at the final stages (**I-V**). Eeva-Stiina Tuittila participated in theoretical and practical planning of the substudies **IV-V** and the preparation of the manuscripts **IV-V** at the final stages. Veikko Kitunen was responsible for carrying out of the gas cromatograph analyses of the substudies **II** and **IV** and he also participated in writing the section "Material and methods" in substudies **II** and **IV**. Marjut Karsisto participated in the preparation of the manuscript **III**, and Kristiina Regina the manuscript **II**, at the final stages.

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DEFINITIONS

Mire is an undrained wetland ecosystem in which organic matter derived from mire plants is accumulated as peat because of poor decomposition due to the high water table.

Peatland is a land where the soil formed is peat. The definition includes undrained mires and the lands drained for forestry or agricultural purposes, where significant peat accumulation no longer occurs.

Restored peatland buffer is a former peatland drainage area restored for water protection purposes to form a buffer between active forestry land and a water body. Restoration is done by blocking the ditch network and clear-cutting the forest stand, and thus the functional mire ecosystem where peat is being formed and accumulated is restored.

Constructed wetlands are generally used to decrease nutrient leaching form agricultural land. They differ from restored peatland buffers in that they are necessarily not peatlands and are much more intensively managed water purification systems. They can be constructed, for example, by digging a pool, in which highly nutrient accumulative vegetation is planted and chemicals added to adsorp nutrients. In contrast to peatland buffers used in practical forestry, vegetation may also be harvested to remove accumulated nutrients from the system.

ABSTRACT

Before large-scale drainage of peatlands for forestry purposes started in the 1950s in Finland, the out-flow water from forests was naturally filtered through pristine mires. Because most mires have now been drained for forestry, especially in southern Finland, and their filtration properties have been lost, suitable buffer peatlands for interacting nutrient loads are being created from drained peatlands. This is done by restoring sections of peatlands drained for forestry by rewetting and clear-cutting the forest stand.

The aims of this study were to study the processes connected to nitrogen and phosphorus removal from through-flow waters in constructed peatland buffers and to quantify the total N and P removal capacity of a restored, nutrient-poor buffer after artificial addition of N and P. One important plant species in nutrient retention in nutrient-poor peatlands has been shown to be cottongrass (*Eriophorum vaginatum* L.). It has a highly developed tolerance to low resources and a high competitive ability in disturbed ecosystems. Special interest was therefore focused on the effect of *E. vaginatum* on nutrient cycling in restored peatland buffers.

Nitrogen and phosphorus was added continuously during June − August in 1999, applying $Ca(NO_3)_2$ (110 kg Ca; 90 kg N ha^{-1}) and K_3PO_4 (38 kg K; 30 kg P ha^{-1}) containing water solution in the experimental area through a feeder ditch. The addition was scaled so that the N and P increase was approximately 100 times higher than the natural level, simulating the release of N and P from the upstream drainage area or upland forest after NP fertilisation or N and P–releasing forestry operations (N and P from decomposing logging residues, especially from needles). Part of the area was left as a control. Nutrient transport and retention in different components of the buffer were monitored in the site in 1998-2001.

Only ca. 0.5% of added N and only ca. 7% of added P was leached through the buffer during the period 1999−2001. The results showed that ca. 15% of added N was removed in the gaseous form and ca. 15% and 70% were retained in the microbial biomass and in the vegetation during the first year after addition, respectively. For the added P the retention percentages were ca. 25%, 25% and 43% in the microbial biomass, vegetation and peat matrix, respectively. However, the results from the second year after N and P addition indicated that the retention of N and P in restored peatland buffers may be significant only in the short-term (during the first year) and that retention is at least partially reversible.

According to the results of this study a restored peatland buffer can remove both N and P from through-flow water. The long-term retention rates of restored peatland buffers may necessarily not be particularly high, but in the case of suddenly increased transient nutrient loadings, retention may be substantial. However, because this study covered only one study site and only a three years' monitoring period a larger study with several sites and longer monitoring period is needed. The studies concerning the role of *E. vaginatum* in nutrient cycling in restored buffers indicated that *E. vaginatum* may play an important role in long-term nutrient retention and moderates the emissions of N_2O by reducing the amount of NO_3^- available for denitrifying micro-organisms.

Key words: gaseous nitrogen loss, nitrogen, microbes, nutrient retention, peatland restoration, phosphorus, vegetation, water protection

CONTENTS

Nutrient retention in a restored peatland buffer

1 Introduction

1.1 Background

Boreal landscape is a mosaic in which upland forests, peatlands and water bodies form a moisture gradient. The outflow waters from upland forests were in most cases filtered naturally through pristine mires before the large-scale drainage began in 1950s in Finland (Keltikangas *et al.*, 1986). The present peatland drainage area represents 53% of the total peatland area in Finland, and in southern Finland the proportion of drained peatlands is as high as 75% (Hökkä *et al.*, 2002).

Forestry operations i.e. cuttings (Ahtiainen, 1990, 1992, Hyvönen *et al.*, 2000, Nieminen 2003, 2004), ditch network maintenance in forested peatlands (Joensuu *et al.*, 2002) and fertilisations (Nieminen, 2000) release nutrients, especially nitrogen (N) and phosphorus (P), to downstream water bodies. According to Kauppila and Bäck (2001) ca. 14% of the total Finnish load of P and 2% of N to the Baltic Sea are from forestry, while the corresponding figures for agriculture are 30% for P and 27% for N. The load of phosphorus from forestry is estimated to be of the same level as that in urban and rural waste waters but that of nitrogen to be ten-fold less (Kauppila and Bäck, 2001). In unpolluted headwater catchments almost all observed anthropogenic N and P load may be due to forestry operations (Laine, 2001).

The detrimental effects of forestry operations on water bodies, especially eutrophication, have gained increasing importance in recent years (Sallantaus *et al.*, 1998). The most serious effects caused by eutrophication are cyanobacteria bloomings and water quality deterioration for aquatic flora and fauna (Kauppila and Bäck, 2001). In headwaters, concern regarding the survival of brown trout (*Salmo trutta* L.) has also been expressed (Laine, 2001).

Sedimentation ponds have long been used for water purification in practical forestry (Joensuu, 1997). Sufficiently large and correctly dimensioned sedimentation ponds are capable of retaining over 90% of the suspended solids entering the pond, but their efficiency in retaining dissolved nutrients is negligible (Joensuu, 1997, 2002). Peatland buffers may be more efficient in retaining dissolved nutrients than sedimentation ponds (Surakka and Kämppi, 1971; Sallantaus *et al.*, 1998).

1.2 Peatland buffers

The idea of purifying waste waters by conducting into pristine mires was a subject of active research in 1960's – 1980's. Surakka and Kämppi (1971) reported the average N retention of 62% and average P retention of 39% in several municipal waste water infiltration peatlands in Finland during several years. In the study of Ihme *et al.* (1991) the N retention was 38-74% and P retention of 37-68% during three years in overland flow areas in northern Finland. Also higher retention percentages (93% for N and 98% for P) were reported by Dubuc *et al.* (1986) during five months in a domestic wastewater infiltration peatland in Quebec, Canada. Thus, peatland buffers are, at least in some cases, capable of retaining nutrients quite effectively from through-flow water.

Since most peatlands have been drained for forestry, especially in southern Finland (Keltikangas *et al.*, 1986), suitable buffer peatlands for interacting nutrient loads from

forested catchments are now being created by restoring sections of drained peatlands (Sallantaus *et al.,* 1998). Formerly, the even topography, dense moss cover and favourable physical, chemical and microbiological properties of surface peat in pristine mires facilitated the removal of N and P from the through-flow water (Ihme *et al*., 1991; Sallantaus *et al.*, 1998). Restoring drained peatlands, may also restore these favourable physical, chemical and microbiological properties that have been lost (Sallantaus *et al*., 1998).

1.3 Mechanisms controlling nutrient removal from through-flow water in restored peatland buffers

1.3.1 Nutrient retention in vegetation

The retention of nutrients in vegetation is dependent on the growth and nutrient uptake of plants, and thus strictly restricted to the growing season. The nutrient retention in the growing season, however, is important from the viewpoint of water protection, because the detrimental effects of eutrophication on the receiving water bodies are usually the most severe during the warm period of the year (Adamus and Stockwell, 1983).

Plants have shown to be effective in retaining especially N but also P from applied fertilisers in boreal peatlands (Päivänen, 1970; Finér and Nieminen, 1997). In addition to being effective in nutrient accumulation, plants also prevent the erosion of surface peat, provide good conditions for physical filtration, insulate against frost during winter, and provide a huge surface area for microbial growth (Liu *et al.*, 2000; O'Donnell *et al*., 2001). However, such processes as nutrient uptake and the ability of plants to retain nutrients in the long-term are still poorly understood (Huttunen *et al*., 1996). Determining the nutrient retention capacity of plants has proven elusive because of the difficulty in quantifying N and P uptake, storage, cycling and release from the plants (Richardson *et al*., 1999).

Results from annually harvested constructed wetlands have shown that they are capable of retaining high amounts of nutrients, especially inorganic N, in suitable conditions (Peterson, 1998). However, without annual harvesting of plant biomass the nutrient retention efficiency of constructed wetland buffers may be very short-term (Peterson, 1998). As vegetation will not be harvested from the buffer zones used in practical forestry, their long-term nutrient retention rates may not be particularly high, but in the case of suddenly increased transient nutrient loadings, retention may be substantial (Sallantaus *et al.,* 1998).

High nutrient inputs into peatland buffers may affect nutrient retention not only by increasing nutrient uptake by the existing vegetation but also by altering vegetation community structure (Bowman and Bilbrough, 2001).

1.3.2 Special case: *Eriophorum vaginatum*

One important plant species in nutrient cycling in nutrient-poor restored peatland buffers may be cottongrass (*Eriophorum vaginatum* L.) (Heikkilä and Lindholm 1997; Komulainen *et al.*, 1998, 1999). It is a perennial, tussock-forming sedge (Polozova, 1970; Wein, 1973; Archer and Tieszen, 1983), which has a high nutrient retention capacity because of its effective biomass production and a nutrient storage system mainly based on stems and leaf sheaths (Shaver *et al*., 1986), the sequential pattern of leaf production through the growing season (Jonasson and Chapin, 1985) and the long lifespan of individual tussocks (122-187 years) (Mark *et al*., 1985).

Cottongrass is a very deeply rooted species and its nutrient uptake efficiency is largely based on this property (Chapin *et al.*, 1979). In late growing season over a half of the nitrogen and phosphorus in cottongrass can be in stems and root system (Chapin *et al.* 1986). Cottongrass may form a long-term sink for nutrients, since the well recognizable residues of dead organs (leaf sheaths and roots) can be found in the peat layers formed thousands of years ago (Mäkilä, 1994).

Cottongrass has a highly developed tolerance to low resources and a high competitive ability in disturbed ecosystems (McGraw and Chapin, 1989; Thormann and Bayley, 1997). It can rapidly become dominant after restoration of cut-away peatlands (Tuittila *et al*., 2000) and peatlands drained for forestry (Heikkilä and Lindholm 1997; Komulainen *et al.*, 1998, 1999). It also colonises suitable peatland sites after wild fire (Wein and Bliss, 1973; Keatinge 1975). In addition, it has a peak in abundance in peatland sites drained for forestry in certain phase in drainage succession (Laiho, 1996), as well as in succession after clear-cuts (Kuusipalo and Vuorinen, 1981) and fertilisations (Päivänen, 1970). It is a typical opportunistic plant species, which has high nutrient use efficiency under low-nutrient conditions (Thormann and Bayley, 1997) and high nutrient uptake efficiency in high-nutrient conditions (Shaver *et al*., 1986). Consequently, cottongrass may be a key plant species in vegetational nutrient retention in restored peatland buffers.

One important question in the role of E. v. on nutrient cycling in restored peatlands is its effect on the strong greenhouse gas N_2O. It has been shown that plants can act as a conduit for the emissions of N_2O (Fey *et al.*, 1999), but, on the other hand, they can compete with denitrifying microbes for inorganic N, and thus reduce the emissions of N_2O (Wang and Bakken, 1997; Korsaeth *et al.*, 2001). Whether the presence of E.v. increases or decreases the emissions of N2O is not understood.

1.3.3 Microbial use of N and P

1.3.3.1 N loss in gaseous form

Northern peatlands contain up to 30% of the total organic nitrogen reserves in the world's soils, and thus have a potential to exert a significant influence on the global atmospheric budget of nitrous oxide (N_2O) (Martikainen *et al.*, 1993). Microbial N_2O production, primarily through nitrification and denitrification processes, may be a substantial fraction of the total N loss from peatlands (Jacks *et al*., 1994), either directly as N_2O or, after further reduction, as dinitrogen (N_2) (Allen *et al*., 1996; Koops *et al*., 1997). Large losses of N in gaseous form are commonly related to waterlogged conditions combined with high N mineralisation rates (Grootjans *et al*., 1985). Thus, N loss in the gaseous form may be a significant mechanism in the removal of N from the restored peatland buffer. Restored peatland buffers may emit considerable amounts of N_2O into the atmosphere, thus enhancing the greenhouse effect and the depletion of stratospheric ozone, especially if there are large amounts of NO_3^- present in the soil water. However, only small areas of peatlands will be restored for water quality protection purposes compared with the whole peatland area in northern, boreal zones, and the total increse in N_2O emissions will therefore be low.

Denitrification is the most important N_2O producing process in waterlogged nutrient-rich peat soils (Velthof and Oenema, 1995), where O_2 is limited and NO_3^- and C are available for micro-organisms (Regina et al., 1996). Denitrification is an anaerobic microbiological process in which C is an energy source and NO_3^- is an electron acceptor, and the denitrification activity is mainly involved with the bacteria

genera *Pseudomonas*, *Micrococcus*, *Bacillus* and *Thiobacillus* (Focht and Verstraete, 1977). In the denitrification process NO_3^- is reduced to the gaseous N compounds N_2O and N_2 (Focht and Verstraete, 1977).

N_2O can also be formed during nitrification, i.e. oxidation of NH_4^+ (Koops *et al*., 1997). The optimum for N_2O production in nitrification is at 50% water filled pore space (Davidson, 1993). Up to 35% of the total gaseous N loss from agricultural land is through N_2O production by nitrification (Hendrickson *et al*., 1980).

NO_2^- is an intermediate product in both nitrification and denitrification processes (Koops *et al*., 1997). Reduction of NO_2^- from nitrification is called nitrifier-denitrification, and this pathway will also lead to the production of N_2O and N_2 (Koops *et al*., 1997).

1.3.3.2 Nutrient retention in microbial biomass

In peat soils, the micro-organisms that are most active in chemical immobilisation of N and P are usually scarce, but they flourish when nutrients are added (Gyllenberg and Eklund, 1974; Jenkinson and Ladd, 1981). Microbes in the surface peat can act as a NO_3^- (Brooks and Zibilskie, 1983) and PO_4^{3-} (Rock *et al.*, 1984) sink from infiltration water in pristine mires. The main bacteria groups in nitrate (NO_3^-) rich conditions are denitrifying bacteria (Alexander, 1961; Jenkinson and Ladd, 1981).

The microbial biomass represents an important reserve of nutrients in soil (Joergensen and Scheu, 1999; Thirukkumaran and Parkinson, 2000). However, there is little quantitative information concerning the potential microbial nutrient uptake in luxurious nutrient conditions (see, however Schmidt *et al*., 1999), especially in wet, acid peat soils (Brake *et al*., 1999; Baum *et al*., 2003), such as peatland buffers, since major part of studies on N and P additions have been done in agricultural soils (Kaiser *et al*., 1995; Chen et al., 2002) or in mineral soil forests (Pietikäinen and Fritze, 1995; Blume *et al*., 2002; Haubensak *et al*., 2002). Microbial growth in soils is typically resource limited and growth increases rapidly in response to added C, N or P; in mineral soils the limiting factor is often the shortage of C compounds (Schmidt *et al*., 1999; Tiquia *et al*., 2002), sometimes also the shortage of N (Peacock *et al*., 2001). In peat soils where C is highly available for microbes, the limiting factors are often low amounts of N or P (Brake *et al*., 1999; Baum *et al.*, 2003).

1.3.4 Nutrient retention in peat matrix

The physical and chemical properties of surface peat can also be important in the nutrient retention in restored peatland buffers. The specific area of peat is large (>200 $m^2\ g^{-1}$) and its porosity is high (90-97%) (Puustjärvi, 1983). The large specific area and porosity increase the cation exchange capacity (CEC) and thus also the nutrient retention capacity, especially for NH_4^+ (Heikkinen *et al.*, 1995). Peat matrix is able to retain only negligible amounts of NO_3^- (Black, 1968) and PO_4^{3-} retention varies substantially depending on site characteristics (Kaila, 1959, Cuttle 1983, Nieminen and Jarva 1996).

Phosphorus retention in acid peat matrix, such as in peatland buffers, is largely governed by the aluminium and iron phosphate formation (Kaila, 1959; Nieminen and Jarva, 1996; Uusi-Kämppä *et al.*, 2000). In phosphate formation from one to three of the hydrogen ions (H^+) of phosphoric acid are replaced by metallic cations, i.e. mostly Al^{3+}, Fe^{3+} or Ca^{2+} (Black, 1968). In soils above pH 7, calcium phosphates should be dominant, while in acid soils iron and aluminium phosphates are the dominant forms (Barber, 1984). Some iron phosphates (e.g. vivianite) are in a strongly immobilised form in peat, and thus their retention may be long-term (Virtanen, 1994). However,

anaerobia is known to inhibit P retention due to the reduction and redistribution of Fe (Armstrong, 1975). Easily soluble phosphate in peat increases by waterlogging, and the increase is greatest is soils with large amounts of iron phosphate (Mahapatra and Patrick, 1969). Thus, P adsorption by restored peat soils is not necessarily a permanent sink for P; it is at least partially reversible (Nichols, 1983). Additionally, P retention capacity of organic soils to that of mineral soils is usually lower (Nichols, 1983).

2 Aims of the study

The Finnish national water protection programme aims at decreasing the nutrient loads from forested areas until 2005 by 50 % from the level of 1993. Thus, in the future, the control of the detrimental effects of forestry operations on water bodies will become increasingly important. One of the means in controlling nutrient leaching is to restore sections of drained peatlands for creating buffer zones between forest land and water bodies. In this study, N and P were artificially added in a restored peatland buffer with the aim (1) to study the main processes controlling N and P removal from through-flow water, (2) to quantify the total N and P retention efficiency of a restored peatland buffer, and (3) to study the effect of *E. vaginatum* on N and P cycling in restored peatland buffers.

3 Materials and methods

3.1 Characteristics of the experimental site and experimental design

Material was collected from a peatland site in central Finland (61°48'N, 24°17'E) that had been drained for forestry in the 1950s and restored in 1995 by rewetting the site by blocking the ditches and clear-cutting the forest stand (Komulainen *et al*., 1998, 1999). The original mire site type before forest drainage had been oligotrophic tall-sedge pine fen (for mire site type description see Laine and Vasander, 1996) which is the most widespread mire site type in Finland (Keltikangas *et al.*, 1986). The constructed peatland buffer area amounts to ca. 15−25% of the water catchment area above. The water catchment area was estimated by using map and levelling measurements in the field. However, because of the artesian discharge water from the near Vatiharju esker, the exact boundaries of the catchment cannot be estimated.

Artificial N and P addition was given continuously during June − August in 1999, applying $Ca(NO_3)_2$ (110 kg Ca; 90 kg N ha^{-1}) and K_3PO_4 (38 kg K; 30 kg P ha^{-1}) containing water solution into the experimental area. The water-soluble fertilisers were dissolved in ditch water in a barrel equippep with adjustable tap, and conducted then into a feeder ditch (Fig. 1). The addition was scaled so that the N and P increase was approximately 100 times higher than the natural level, simulating the release of N and P from upstream drained peatlands or upland forests after NP fertilisation or N and P–releasing forestry operations (N and P from decomposing logging residues, especially from needles) (Kenttämies, 1981; Hyvönen *et al*., 2000; Nieminen, 2003).

There was a height difference of 0.8 m in 70 m distance between the upper and lower experimental areas (1.14% gradient) and the N and P increase in the lower area was received through hydrologic transport via the upper experimental area. Water input into the area was conducted via two ditches (Fig. 1). One ditch was used as the N and P feeder ditch discharging into the experimental areas while the other ditch flowed into the control area (Fig. 1).

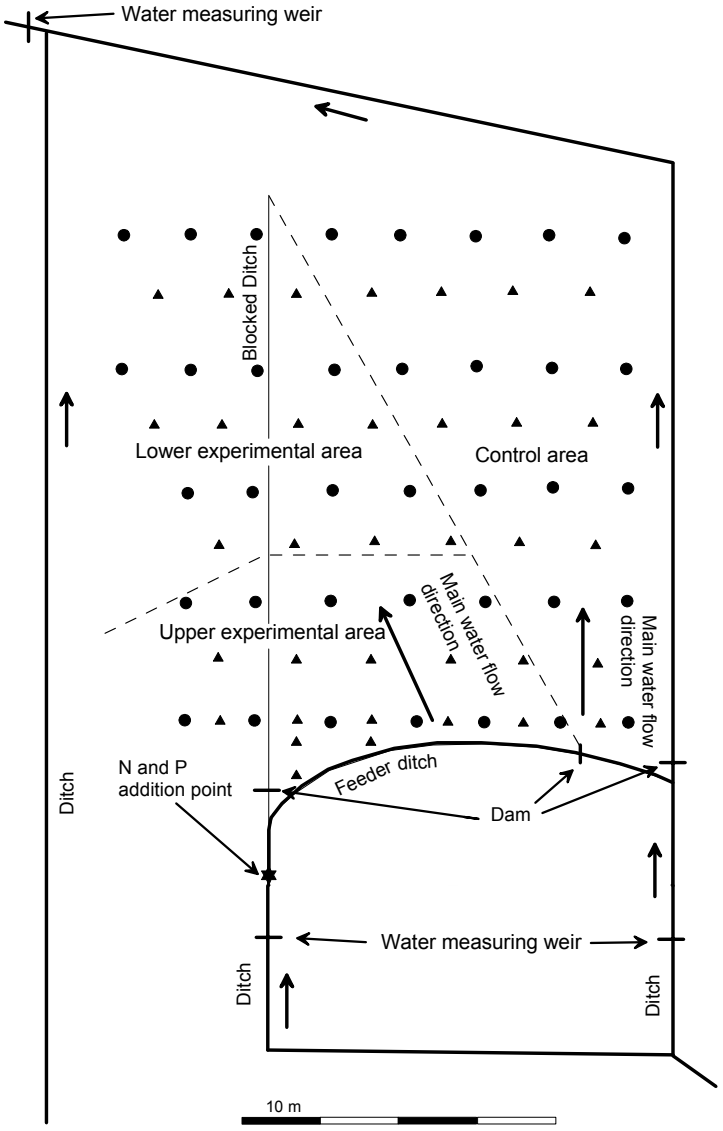

Figure 1. Schematic map of the location of the three experimental areas relative to each other. N and P addition point, feeder ditch and main water flow directions in the study site are shown. Filled circle is the water sampling well and filled triangle is the plant biomass sampling plot (35 plots). From 19 of the plant biomass sampling plots was collected also the above ground biomass in addition to below ground biomass.

The soil is rather humified *Carex*-peat (H4-H6 according to the scale of von Post; Puustjärvi, 1970), and the thickness of the peat layer is over 2 m (Jauhiainen *et al.*, 2004).

The long-term annual mean temperature of the area is 3.6 ºC, and the temperature sum of the area is ca. 1150 degree days (threshold value +5ºC). The mean annual precipitation of the area is ca. 650 mm and the mean precipitation during growing season ca. 330 mm. The mean annual NO_3^- deposition in the area is ca. 1.7 kg ha^{-1} and NH_4^+ ca. 1.25 kg ha^{-1} (total N deposition ca. 2.8 kg ha^{-1}) (Finnish Meteorological Institute, 1999).

The experiment was carried out by using 1998 as a calibration period with no NO_3^- or PO_4^{3-} addition. Part of the site was left as a control area (ca. 0.3 ha). The upper experimental area, which received high NO_3^- and PO_4^{3-} additions from the feeder

ditch in 1999, had an area of approximately 0.2 ha. The lower experimental area which got a lower NO_3^- and PO_4^{3-} addition through the upper area was approximately 0.3 ha. Boundaries of the areas were determined after N and P addition on the basis of the concentrations of NO_3^- and PO_4^{3-} in soil water.

3.2 Measurement of nutrient transport

The hydraulic load and nutrient transport were monitored in the site in 1998-2001. Hydraulic load rates were measured using a triangular Thompson's (90°) measuring weirs equipped with a limnigraph allowing continuous measurements. Limnigraphs and weirs were insulated allowing hydraulic load measurements also during winter. Water samples were taken monthly from the overflow of the weir above and below the constructed peatland buffer. NO_3^- and PO_4^{3-} were analysed from filtered water samples (0.45 μm Millipore) with Tecator 5020 FIA analyser in the Environmental Centre of Pirkanmaa and K and Ca with ARL 3580 ICP analyser in the Finnish Forest Research Institute. The nutrient transport rates (g ha-1) were calculated by multiplying the hydraulic load rates with the nutrient concentrations in water and integrating the values over the study period.

For determining inner spatial variation in NO_3–N, PO_4–P, K and Ca concentrations in soil water in the buffer, water samples were also taken from 37 systematically situated water wells. The samples were taken monthly during the growing seasons 1998, 1999 and 2000, and analysed as above.

3.3 Plant biomass and nutrient retention

Biomass of the above-ground parts of the plants was investigated at the time of the peak standing biomass in August yearly in 1998-2000. The above-ground plant biomass was harvested and analysed in five groups, i.e. sedges, herbs, shrubs, cottongrass and bryophytes. The cottongrass group was divided into living leaves and stems and leaf sheaths and corresponding dead parts (Wein, 1973). The bryophytes group was divided into Sphagna and other bryophytes. The plant biomass was harvested from 19 systematically located biomass sampling plots with an area of 0.5 m^2 for vascular plants and 0.25 m^2 for bryophytes. Plant nomenclature followed Moore (1982) for vascular plants and Koponen *et al.* (1977) for bryophytes.

The below-ground biomass was collected simultaneously with the above-ground biomass from 35 systematically distributed peat monoliths (8×8×50 cm) down to a depth of 50 cm. The monoliths were then divided into two parts: 0-25 cm and 25-50 cm. Roots with a diameter of >0.5 mm were separated out manually and divided into the living and dead roots of cottongrass and living and dead roots of the other plant species.

The collected biomass components were oven-dried at 60°C and the above ground biomass components were measured separately for each of the 19 sample plots and the below-ground biomasses for each of the 35 peat monoliths. Prior to chemical analyses, the biomass samples from different plots and peat monoliths were combined to give one sample for each biomass component in each of the three experimental areas. The samples were then homogenized, digested in HNO_3–H_2O_2 solution and analysed for total N, P, Ca, K and Mg (**I**). Nutrient contents in each plot (g m-2) were calculated as the product of the pooled nutrient concentrations (the samples from different plots at each of the three areas combined) and biomass dry weight of each individual plot.

3.4 Gaseous N loss

Total N loss in gaseous form from peat soils can be quantified by using the ^{15}N-technique or the C_2H_2 inhibition technique (Mosier and Klemedtsson, 1994). In this study the latter technique was used because it is simpler, cheaper and more commonly used. This technique is based on C_2H_2 selectively inhibiting N_2O reduction to N_2, enabling the total N flux to be measured as N_2O (Davidson *et al.,* 1986; Koops *et al.,* 1997).

Experimental design and gas sampling was carried out as described in **II**. Nine gas samples were taken over 3.5 h from the headspace of the chamber into 60 ml plastic syringes closed with a three-way stopcock (Nykänen *et al.,* 1995). Four samples were taken before C_2H_2 addition (5, 20, 35 and 50 min after closing the chamber) and five samples after 10% C_2H_2 addition into the headspace of the chamber (90, 120, 150, 180 and 210 min after closing the chamber). The N_2O and C_2H_2 samples were analysed as described in **II**.

During collecting of gas samples the water table level and peat temperature was measured close to each chamber. At approximately 3 weeks intervals soil water samples were collected near the chambers. NO_3^- concentrations in the water samples were analysed with a Tecator 5020 FIA analyser.

Annual N losses through N_2O emission were determined by linear integration of the N_2O production rates.

3.5 Nutrient retention in microbial biomass

The same 8×8×50 cm peat monoliths as used for the below ground plant biomass calculations were also used in the microbial N and P uptake study (**I**, **III**). All samples were adjusted to a water content of 60% and stored at 4°C before analyses (Joergensen, 1996). Microbial C (Vance *et al.,* 1987), N (Brookes *et al.,* 1985) and P (Brookes *et al.*, 1982) were measured with fumigation-extraction method using 4 replicate samples of fresh peat equalling 2 g dry mass (**III**). Microbial C, N and P (C_{mic}, N_{mic} and P_{mic} μg g^{-1} peat dry mass) were then calculated using the equations shown in **III**.

3.6 Nutrient retention in peat matrix

N, P, Al and Fe concentrations in peat were analysed from the same peat samples as used in the microbial biomass study (**III**) and for the below-ground biomass calculations. For total nutrient analyses, the samples were dry combusted and the ash taken up in HCl. The samples were analysed for total P, Al and Fe by ICP ARL 3580 analyser and total N by Leco CNS 1000 analyser in the Finnish Forest Research Institute.

3.7 Special case: Eriophorum vaginatum

3.7.1 Nutrient retention in *E. vaginatum*

3.7.1.1 Greenhouse experiment

The temporal growth pattern, above- and below-ground biomass allocation of cottongrass and its nutrient retention dynamics were investigated in a greenhouse

experiment, and the temporal growth pattern also in a field experiment with three N and P addition levels in the constructed peatland buffer.

The greenhouse experiment was conducted to assess the seasonal growth and nutrient retention dynamics of cottongrass in situation with controlled nutrient input (**V**).

In the greenhouse experiment a water-soluble multi-nutrient fertiliser was given with the irrigation water at a concentration of 0.1%, amounting 81 g N m^{-2} and 17 g P m^{-2} during the growing season. Nutrient content (g kg^{-1}) of the multi-nutrient fertiliser used in the greenhouse experiment was 64, 50, 260 and 27 for NO_3^-, P, K and Mg, respectively. Irrigation and outflow water was sampled simultaneously with irrigation at two weeks intervals, and their total N and P concentrations were analysed using Tecator 5020 FIA and ICP ARL 3580 analysers.

The first harvest group was harvested in July, the second in August and the third in November 1999. At each harvest group, living and dead leaf blades, stems and leaf sheaths and roots were separated. The dry masses (at 60 °C) of each separate organ were measured, and the concentrations of N and P were analysed using Leco CNS 1000 and ICP ARL 3580 analysers.

The exsertion, elongation and senescence of leaves from 12 tillers of the third harvest group were measured, and the genesis of new tillers was observed at two weeks intervals, following the method of Shaver and Laundre (1997) and that used in **IV**.

3.7.1.2 Field experiment

The field experiment was conducted to assess the seasonal growth dynamics of individual tillers in three different N and P levels formed by artificial N and P addition through a feeder ditch in the upper end of the site (**I**–**III**). Along the distance from the feeder ditch, a gradient in moisture and nutrients was formed (Table 2 in **V**).

Nine tussocks situated in three groups along a decreasing gradient of altitude, moisture and N and P concentration in soil water were selected for the study. One tiller from each of the nine tussocks was selected for intensive observation of the leaf and tiller growth dynamics, and they were measured as in the greenhouse experiment.

3.7.2 Competition for NO_3^- between *E. vaginatum* and microbes

For determining the competitive effect of NO_3^- uptake by vegetation on N_2O fluxes (**II** and **IV**) a network of 12 plots (60×60 cm) were established in spring 2001. It was aimed creating a data set with wide variation in the NO_3^- concentrations in soil water and cottongrass cover for the model development. The plots were divided into three different cottongrass cover classes. The classes were settled a priori to four plots without vegetation (all vegetation removed, including *Sphagnum*-mosses), four plots with cottongrass initial cover ca. 10% and four with cottongrass initial cover ca. 70%.

The average prevailing (background) NO_3^- concentration in soil water was analysed. Following this four different NO_3^- additions were given, leading to four different concentration levels in soil water: prevailing level of ca. 0.06 mg NO_3–N l^{-1}, 100x addition leading to a concentration of ca. 6 mg NO_3–N l^{-1}, 1000x addition to ca. 60 mg NO_3–N l^{-1} and 10000x addition to ca. 600 mg NO_3–N l^{-1} in soil water. NO_3^- addition was given as KNO_3 water solution (ca. 5 l per plot at one addition) 12 hours before taking N_2O samples. Water used for KNO_3 solution was local ditch water. Prevailing NO_3^- level plots were irrigated with ditch water only without added NO_3^-.

Consequently, we had one plot of each cottongrass abundance class and NO_3^- addition level combinations.

Gas sampling was carried out as described in **II** and **IV**. Soil water samples were collected 10 min after NO_3^- addition and 12 h later just before N_2O sampling from the plots. NO_3^- concentrations (mg l^{-1}) in the soil water samples were analysed with a Tecator 5020 FIA analyser in the Finnish Forest Research Institute.

Almost 100% of the vascular plants in the plots with vegetation consisted of cottongrass. The projection cover was estimated 12 times at 2-4 weeks intervals. Simultaneously with cover estimation, the exsertion, elongation and senescence of leaves of the tillers were measured from five 8×8 cm systematically situated subplots, following the method of Shaver and Laundre (1997). At each measurement date, the length and width of the green part of each leaf, from oldest to youngest, was measured using the end of the leaf sheath as a baseline. The leaf area of cottongrass (m^2 m^{-2}) in the plot was calculated multiplying the measured length and width of leaves by the estimated total leaf count of the plot.

A model (Eq. 1 in **IV**) for the N_2O flux (end product of denitrification) was formulated to analyse the effect of the competition by cottongrass on denitrifying microbes. In this model temperature (T) (average of 10, 20 and 30 cm T) was taken into the model as a background factor (Kaiser *et al.,* 1998; **II**), and the leaf area of cottongrass was used to describe the competition effect.

3.8 Statistical analyses

The differences in N and P concentrations in outflow water, plant biomass, microbial biomass, and peat matrix between different years (1998, 1999, 2000, 2001) and/or the three experimental areas were analysed with one-way ANOVA. The effects of NO_3^- treatment and C_2H_2 addition on N_2O fluxes were analysed with repeated measures ANOVA with C_2H_2 incubation (with C_2H_2/without C_2H_2) and experimental area as grouping factors and sampling date as a within factor. In paper (**V**), repeated measures ANOVA was also used to analyse the effect of N and P addition (grouping factor) and sampling time (within factor) on leaf lenght and tiller number of *E. vaginatum*. The correlation of P with Al and Fe concentrations in peat were studied by calculating Pearson's correlation coefficients. Analyses were performed using the SYSTAT for Windows statistical tool package (SYSTAT, 1999). Contour smoothing in figures 5−8 was calculated using kriging method.

4 Results

4.1 N and P removal efficiency of the restored peatland buffer

The monthly average water input was 0.05–0.7 l s^{-1} in the experimental areas and 0.05–0.5 l s^{-1} in the control area in 1998–2001 (Fig. 2). The monthly average outflow from the area was 0.1–1.5 l s^{-1} (Fig. 2). The water input and outflow were greatest during the spring flood season and lowest in winter.

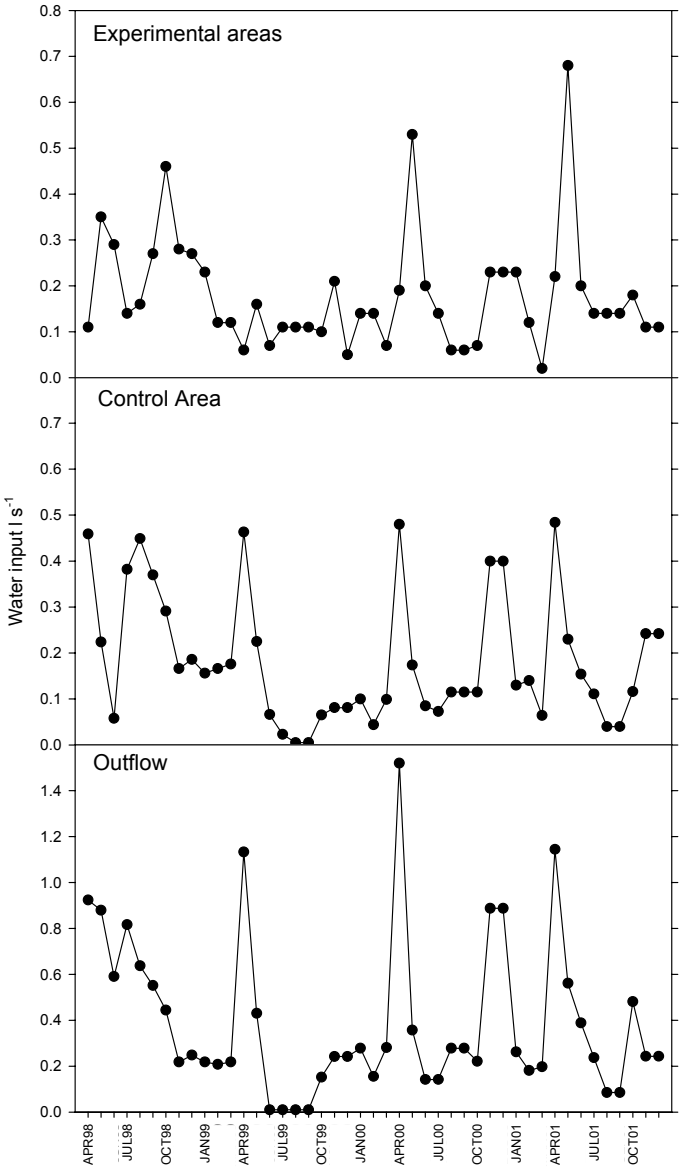

Figure 2. Water input into the experimental areas and control area and water outflow from the areas (l s^{-1}) during 1998-2001.

Background NO_3−N input into the experimental areas before NO_3^- and PO_4^{3-} addition was 8–43 g y^{-1} and background PO_{43}−P input 4–9 g y^{-1}. Corresponding NO_3−N and PO_{43}−P inputs in the control area were 18–67 g y^{-1} and 15–31 g y^{-1}. The background N and P loads in the experimental area were minimal compared to the extra N (45 kg) and P (15 kg) additions given in the growing season 1999. Although N and P additions were high in 1999, the concentrations in outflow water and loads (concentration × runoff) in 1999–2001 remained relatively low (Figs. 3 and 4), except for PO_4^{3-} (Figs. 3 and 4); the concentrations of which in outflow water were high from spring 2000 to late summer 2001.

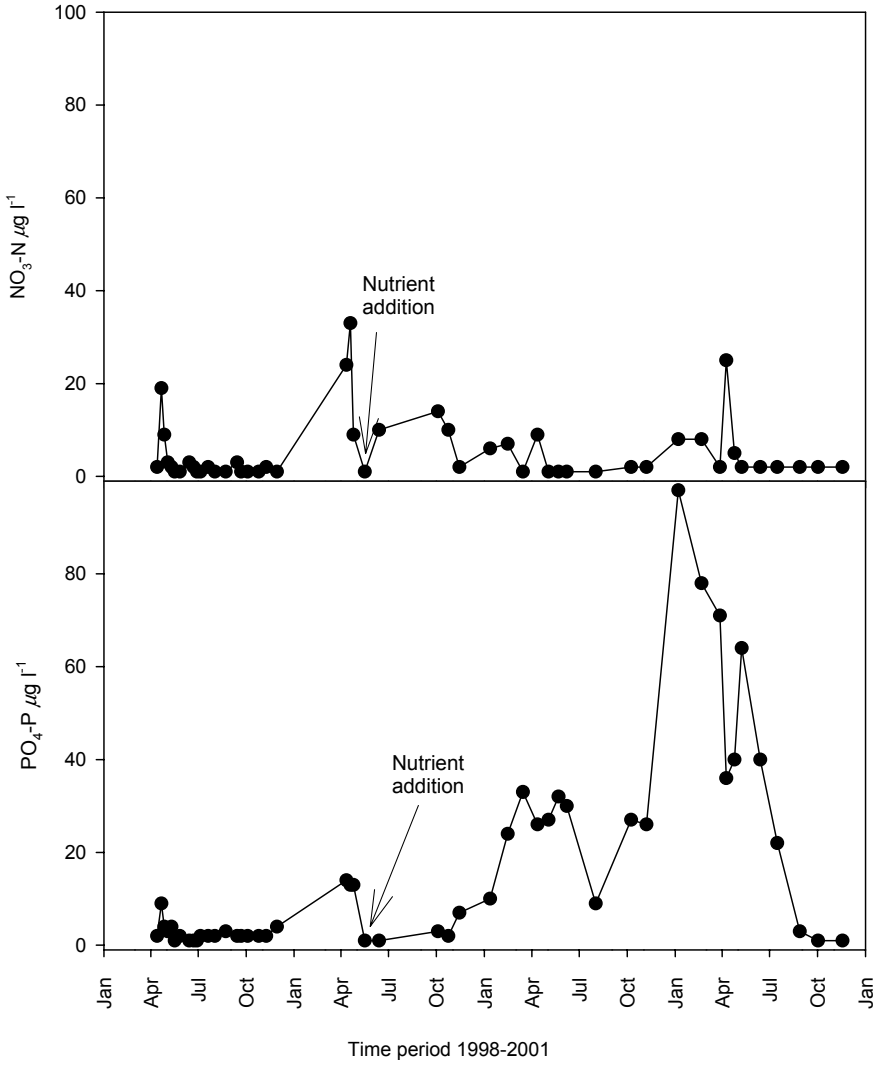

Figure 3. NO_3−N and PO_4−P concentrations (μg l^{-1}) in the outflow water during 1998-2001.

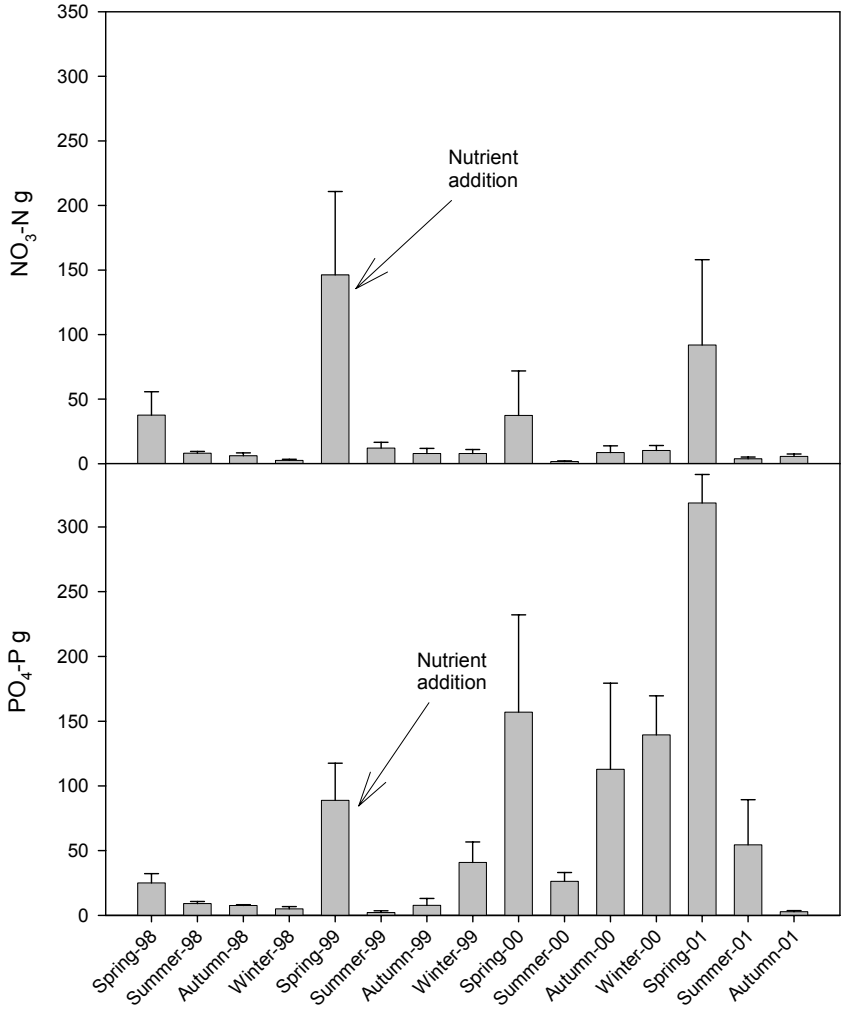

Figure 4. NO_3−N and PO_4−P outflow (g) during three months periods in 1998-2001.

Nutrient movements in the constructed peatland buffer were carefully monitored during 1998–2000 by collecting water samples from a grid of water wells. The results showed that especially the added NO_3^- was retained in the relatively small area in the upper experimental area, ca. 0.2 ha (Figs. 5 and 6), whereas added PO_4^{3-} spread out to a much larger area (Figs. 5 and 6). Also K and Ca spread out to a larger area than NO_3^- (Figs. 5−8).

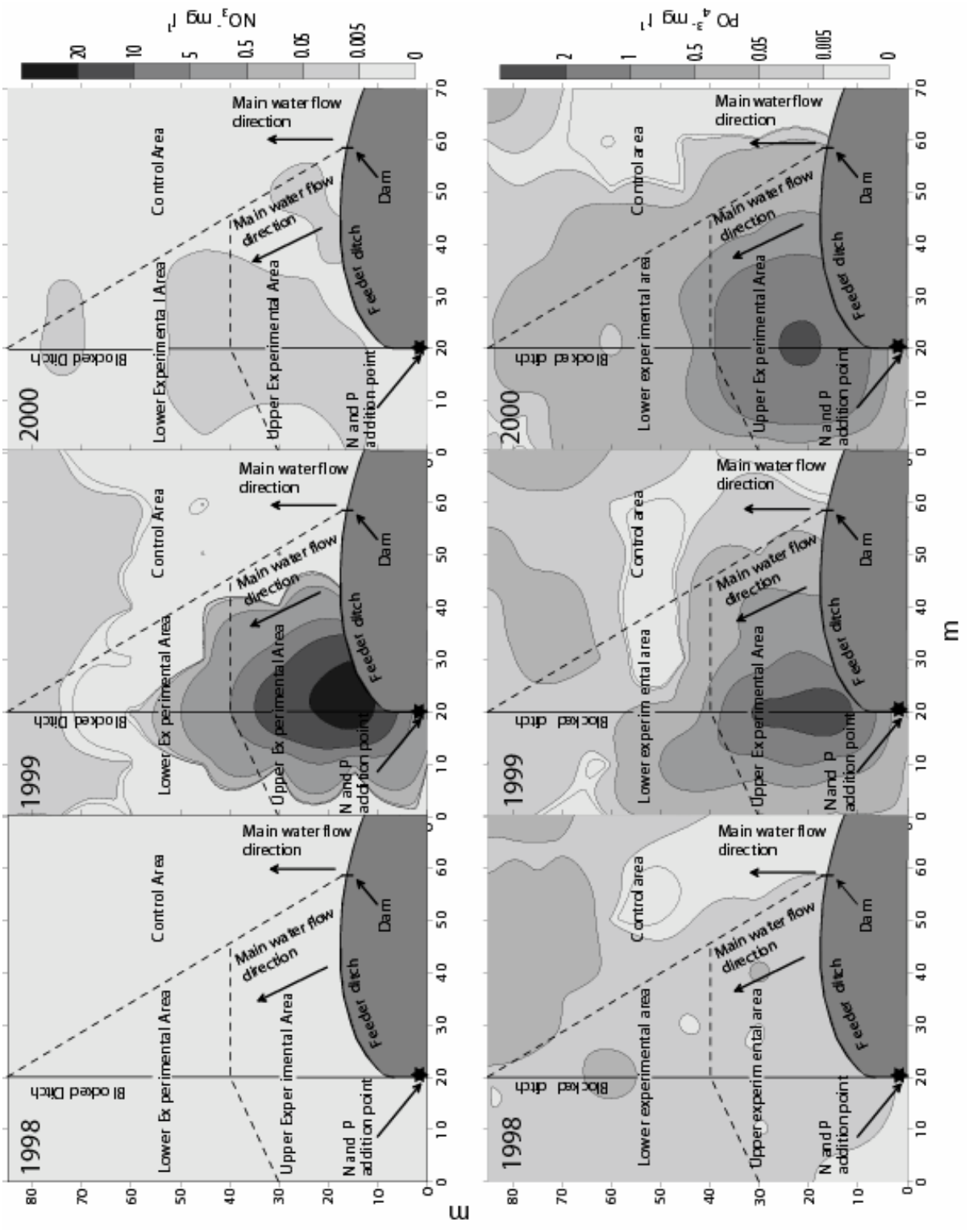

Figure 5. Spatial variation in NO_3−N and PO_4−P concentrations (mg l^{-1}) in soil water in the restored peatland buffer during 1998–2000. The average NO_3−N and PO_4−P concentration values for the summer of each year were calculated from water samples taken 3−4 times during the period.

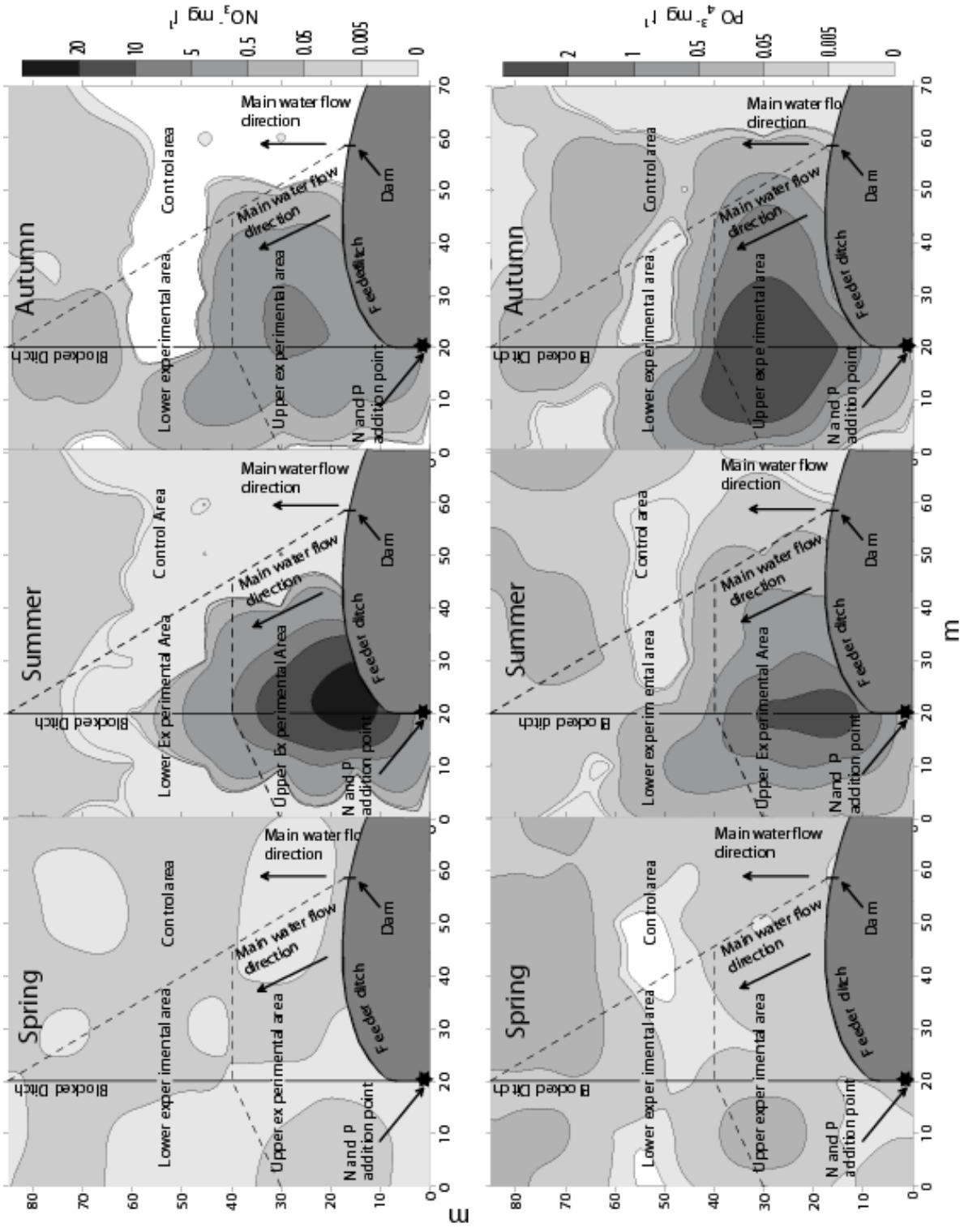

Figure 6. Spatial variation in NO_3−N and PO_4−P concentrations (mg l^{-1}) in soil water in the restored peatland buffer during the growing season 1999. The average NO_3−N and PO_4−P concentration values for spring, summer and autumn were calculated from water samples taken 2−5 times during the period.

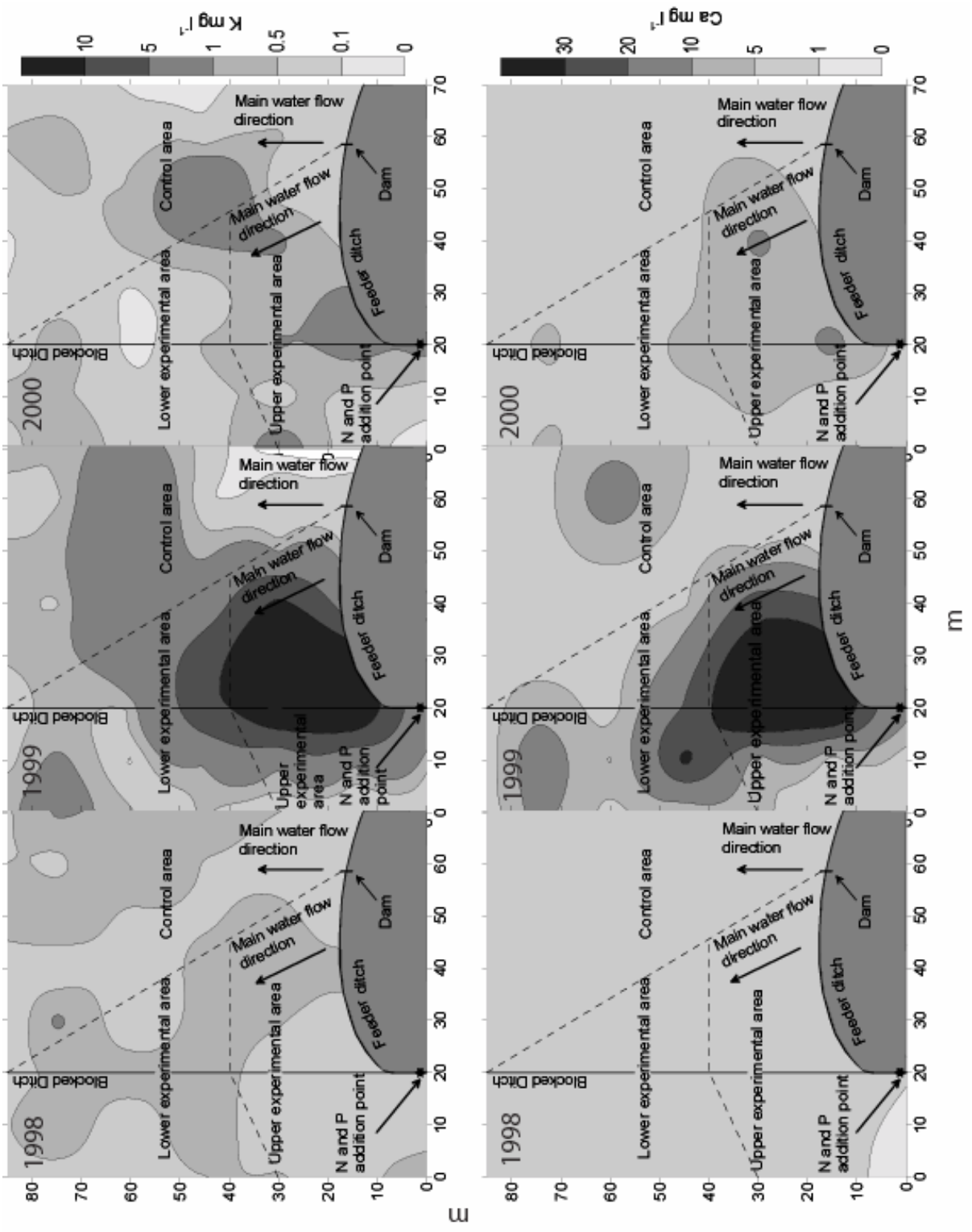

Figure 7. Spatial variation in K and Ca concentrations (mg l^{-1}) in the restored peatland buffer during 1998–2000. The average K and Ca concentration values for the summer of each year were calculated from water samples taken 3–4 times during the period.

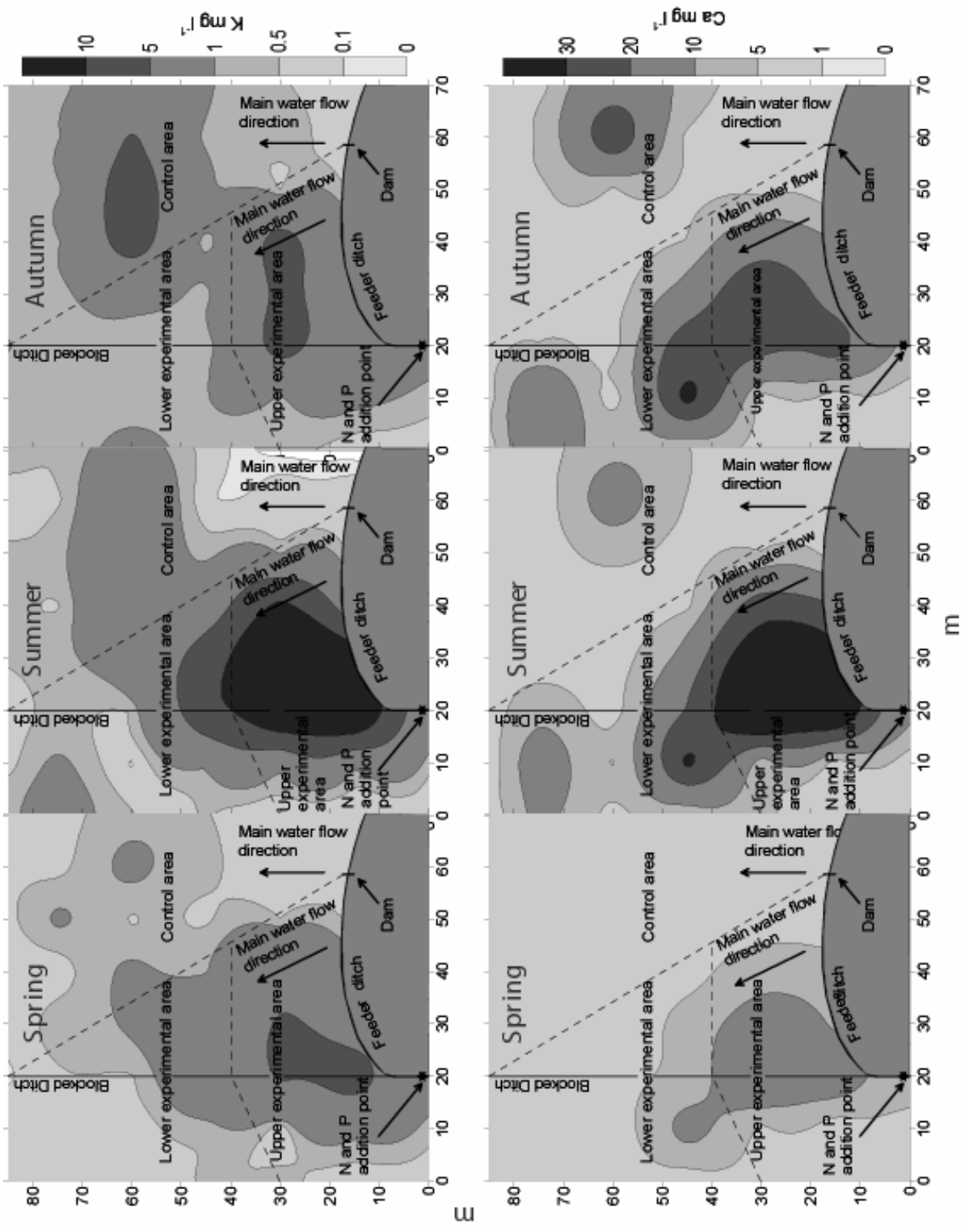

Figure 8. Spatial variation in K and Ca concentrations (mg l^{-1}) in soil water in the restored peatland buffer during the growing season 1999. The average K and Ca concentration values for spring, summer and autumn were calculated from water samples taken 2−5 times during the period.

Only ca. 0.5% of added N and only ca. 7% of added P was leached through the buffer during the period 1999–2001 (Table 1, Fig. 9).

Table 1. The balance sheet of N and P load (natural and artificial), release and retention (kg) in the biological and the geochemical processes in the upper and lower experimental areas combined (U+L) and control area separately. Natural N and P load and release due to nutrient addition was calculated for the period 1999-2001. The N and P release was calculated by subtracting the natural release (release in 1998) from the measured release in 1999-2001.

U+L	Natural load	Addition	Retention				Release from addition
			Peat matrix	Vegetation	Gaseous loss	Microbes	
NO_3-N	0.008 0.043	45.0	0	31.4	5.5	6.8	0.28
PO_4-P	0.004 0.009	15.0	6.8	3.6	0	3.6	1.03
Control	Natural load	Addition	Peat matrix	Vegetation	Gaseous loss	Microbes	
NO_3-N	0.018 0.067	0	0	4.7	1.0	0.1	0
PO_4-P	0.015 0.031	0	0.0	0.5	0	-0.6	0

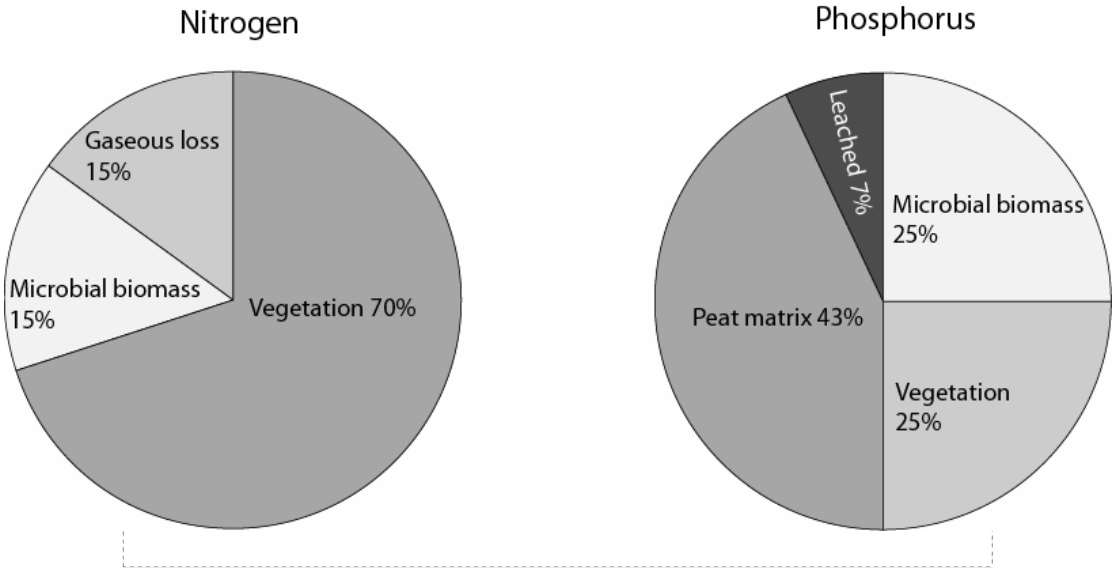

Figure 9. The retention of N and P (%) in the restored peatland buffer by the different biological and geochemical processes during the first year after nutrient addition.

4.2 Processes leading to N and P removal

4.2.1 Plant biomass and nutrient retention

In 1999 the total plant biomass increased by about 20% in the upper experimental area, 2% in the lower experimental area and 7% in the control area compared to the control year 1998 (Fig. 2 in **I**). The biomass and increase in biomass below the ground surface were higher than those above the ground surface (Fig. 2 in **I**). The increase in the mass of dead organs of cottongrass was very rapid: on average 75% between the control year (1998) and 1999 in the upper experimental area (Table 2 in **I**). The greatest absolute increase in the upper experimental area was observed in the above- and below-ground parts of cottongrass and in *Sphagnum* biomass (Table 2 in **I**), but the greatest proportional (%) increase in the above-ground herb biomass (Table 2 in **I**). This is also clearly seen in changes in projection covers: the cover of herbs increased over fivefold, while the cover of sedges (including cottongrass) only ca. doubled (Table 3 in **I**). The most abundant herb species were *Epilobium angustifolium* and *E. adenocaulon,* and the most abundant *Sphagnum* species were *Sphagnum angustifolium* and *S. russowii* (**I**).

There was no increase in the gravimetric N and P concentrations in the plant tissues but the observed increase in the N and P contents in plants was caused by the increase in the plant biomass. In 1999 the total content of N in plants increased about 25% in the upper experimental area, 4 % in the lower experimental area and 6 % in the control area compared to the year 1998 (Fig. 2 in **I**). The dynamics in N contents followed the trends observed in plant biomasses.

In 1999 the total content of P in plants increased about 35% in the upper experimental area, 13% in the lower experimental area and 9% in the control area compared to the year 1998 (Fig. 2 in **I**). The dynamics in P contents also followed the trends and magnitudes observed in plant biomasses.

Total N retention in the plant biomass during the first year after N and P treatment ranged from 126.7 kg N ha^{-1} in the upper experimental area to 20.4 kg N ha^{-1} in the

lower experimental area and 15.7 kg N ha^{-1} in the control area. P retention ranged from 13.1 kg P ha^{-1} in the upper experimental area to 3.4 kg P ha^{-1} in the lower experimental area and 1.8 kg P ha^{-1} in the control area. The retained proportions of N and P in the plant biomass in the two experimental areas were approximately 70% of the added N (45 kg N y^{-1}) and approximately 25% of the added P (15 kg P y^{-1}) during the first year after addition in 1999 (Fig. 9, Table 1).

4.2.2 Gaseous N loss

In the control year 1998, the concentrations of NO_3^- in the water were low (1-2 μg l^{-1}) in all experimental areas (Fig. 4 in **II**). After the NO_3^- addition, NO_3^- concentrations rose to 32 mg l^{-1} in the upper experimental area in early summer of 1999 (Fig. 4 in **II**). In the lower experimental area and the control area NO_3^- concentrations (ca. 10 μg l^{-1}) were also slightly increased (Fig. 4 in **II**). The concentrations of NO_3^- in the upper experimental area decreased rapidly in winter 2000 but stayed at a slightly increased level (ca. 10 μg l^{-1}) in summer 2000, as also in the lower experimental area (Fig. 4 in **II**). In the control area NO_3^- concentrations (ca. 3 μg l^{-1}) were low in 2000 (Fig. 4 in **II**).

The N_2O fluxes (**II)** in spring 1999 increased rapidly (Fig. 3 in **II**) in the upper experimental area, which was situated nearest to the feeder ditch. The fluxes decreased with the decreasing NO_3^- concentrations and soil temperature in winter 2000 but rose to a slight peak again in July-August 2000, (Fig. 3; Table 1 in **II**). This peak was also observed in the lower experimental area (Fig. 3 in **II**). However, spatial and temporal variation was large both within and between the areas (Fig. 3; Table 1 in **II**). The simultaneous variation in the gaseous N fluxes and the mean soil temperature at a depth of 10-30 cm can also be seen clearly in Figs 2 and 3 in **II**.

In 1998 there were no significant differences in N_2O fluxes between the experimental areas, but after NO_3^- addition in 1999-2000, the N_2O fluxes from the upper experimental area were significantly higher than from the lower experimental and control area.

The gaseous N loss measured using acetylene-inhibition method ranged from 5 kg N ha^{-1} y^{-1} in the lower experimental area to 20 kg N ha^{-1} y^{-1} in the upper experimental area and 3.5 kg N ha^{-1} y^{-1} in the control area. The total gaseous N loss from the site was approximately 15% of added N during the first year after addition (Fig 9).

4.2.3 Nutrient retention in microbial biomass

In 1998 there were no significant differences in microbial C, N or P between the experimental areas. N and P addition caused a significant increase in the amounts of microbial C measured in 1999 in the upper experimental area, but only in the peat layer 0-25 cm. There was no significant increase in microbial C, N or P in the other areas. In all areas, the amounts of microbial C, N and P decreased with sample depth (Fig. 2 in **III**). The N and P addition caused no significant increase in microbial C, N and P in the peat layer 25-50 cm in any of the areas. In 2000 the amounts of microbial C, N and P started to decrease with decreasing concentrations of NO_3^- and PO_4^{3-} in the soil water even in the upper experimental area (Figs. 1 and 2 in **III**), but microbial C was still significantly higher than in 1998.

N retention (differences in the amounts in 1998 and 1999) into the microbial biomass during the first year after N and P addition ranged from 30.6 kg N ha^{-1} in the upper experimental area to 2.1 kg N ha^{-1} in the lower experimental area and 0.4 kg N ha^{-1} in the control area. P retention ranged from 13.8 kg P ha^{-1} in the upper

experimental area to 2.8 kg P ha^{-1} in the lower experimental area and –2.3 kg P ha^{-1} in the control area. The proportions of N and P retained in the microbial biomass in the experimental areas were approximately 15% of the added N (Fig. 9) and approximately 25% of the added P (Fig. 9) during the first year after N and P addition in 1999.

4.2.4 Nutrient retention in peat matrix

The differences in peat N and P concentrations (mg g^{-1}) between the experimental areas or years were not significant. However, the peat P content (kg ha^{-1}) was clearly higher in the upper experimental area in 1999 than in the control year 1998 (Fig. 10). Significant positive correlation was observed between the peat P and Al concentration (mg g^{-1}) in each year (r=0.29; P<0.05 in 1998, r=0.42; P<0.01 in 1999 and r=0.32; P<0.01 in 2000). The significant positive correlation was observed also between the peat P and Fe (mg g^{-1}) concentration in each year r=0.37; P<0.01 in 1998, r=0.49; P<0.01 in 1999 and r=0.53; P<0.01 in 2000. Differences in Al and Fe concentrations between the years nor between the areas were not significant. However, Fe concentrations were higher in the control area and lower experimental area than in the upper experimental area (Table 2), where P concentrations were the highest. The same trend could not be seen in Al concentrations (Table 2), at least not so clearly.

Table 2. Average peat Al and Fe concentrations ± SE (mg g^{-1}) in the experimental areas during 1998-2000.

	1998		1999		2000	
	Al	Fe	Al	Fe	Al	Fe
Upper	0.755± 0.049	2.160± 0.222	0.896± 0.103	2.060± 0.255	0.814± 0.089	2.137± 0.177
Lower	0.861± 0.054	2.380± 0.239	0.613± 0.064	2.298± 0.404	0.801± 0.037	2.363± 0.158
Control	0.726± 0.049	2.265± 0.246	0.816± 0.097	2.436± 0.397	0.746± 0.065	2.410± 0.324

The retained proportion of added P in the peat matrix was ca. 43% in 1999 (Fig. 9). The amounts of N in peat did not differ between years or the three experimental areas (Fig. 10).

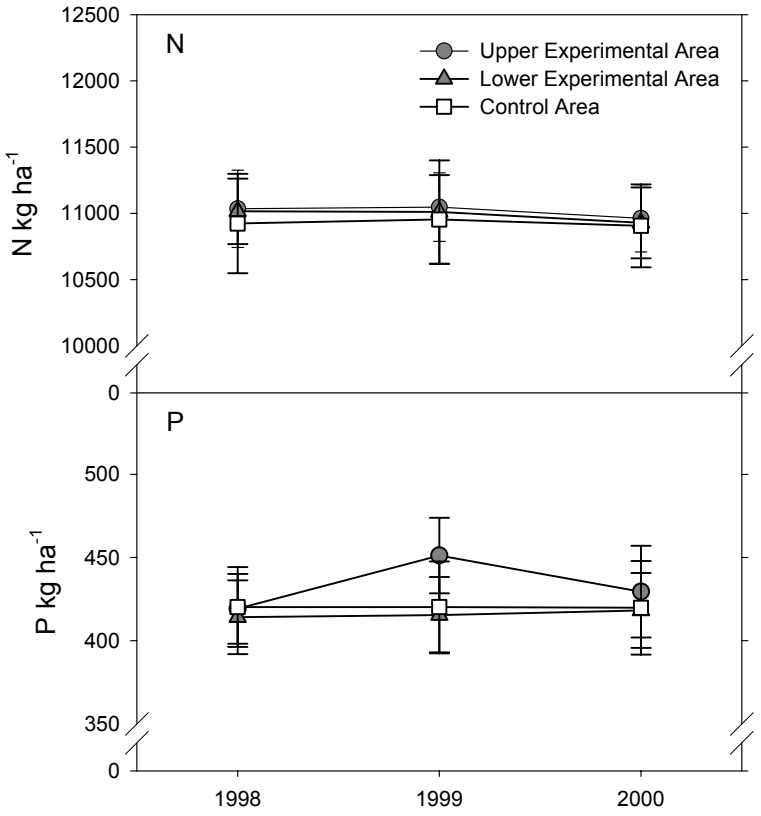

Figure 10. Peat N and P content for 0−50 cm layer (kg ha^{-1}) in the experimental areas during 1998−2000. Vertical bars are SE for means.

4.2.5 Special case: *Eriophorum vaginatum*

4.2.5.1 Nutrient retention in E. vaginatum

The growth dynamics of cottongrass are determined by four processes: (1) the development of leaf cohorts, (2) leaf elongation, (3) new tiller production and (4) root elongation.

The leaves of the 3rd and 4th cohorts never reached the same lengths as the leaves of the 1st and 2nd cohorts (Fig. 1 in **V**). Additionally, the length of the 3rd and 4th cohort leaves decreased along the decreasing N and P concentration and moisture gradient, and the 4th cohort was completely missing in the lower experimental area. Nutrient level affected significantly the total average leaf lengths and also the seasonal pattern in leaf elongation and senescence in the experimental areas in the field.

In conditions with high availability of nutrients and moisture new tiller production increased rapidly from the beginning of the growing season and reached a peak in late July (Fig. 2 in **V**). The total number of tillers produced during the growing season decreased with the decreasing N and P concentration and moisture gradient (Fig. 2 in **V**).

New tiller production followed a rather similar pattern in the greenhouse experiment and in the upper experimental area with similar nutrient and moisture

availability (Fig. 2 in **V**) and the number of new daughter tillers was also rather similar.

There was a positive correlation between the total root (sum of all the roots) and leaf lengths of individual tillers (Fig 3 in **V**) as well as between the total root length and the number of daughter tillers (Fig 3 in **V**).

In the greenhouse experiment, all organs increased in biomass through the growing period (May − November) (Fig. 4 in **V**). In May the greatest dry mass proportion was in living stems and leaf sheaths (Fig. 5 in **V**). In November up to 45% of the dry mass of living organs (Fig. 4 in **V**) and over 20% of the total dry mass (Fig. 5 in **V**) was in roots. In November the greatest dry mass proportion was in dead stems and leaf sheaths (Fig. 5 in **V**).

Except in living leaf blades, the amounts of N and P in the organs of cottongrass increased throughout the growing period (May − November) (Fig. 4 in **V**). In May the greatest N and P proportions, following the biomass, were yet in storage organs: living stems and leaf sheaths (Fig. 5 in **V**).

Differences between the amounts of N and P in irrigation and outflow water indicated a clear accumulation of N and P into cottongrass tissues during the growing period (Fig. 6 in **V**). The immobilised amounts of N and P were 73 g N m^{-2} (91 % of the added N) and 13 g P m^{-2} (77 % of the added P) (Fig. 6 in **V**). At the end of the growing period a clear release of P into outflow water was, however, observed (Fig. 6 in **V**).

4.2.5.2 Competition for NO_3^- between E. vaginatum and microbes

The leaf area of *E. vaginatum* varied from 0 in the peat surface plots without vegetation to over 15 m^2 m^{-2} in the plots where *E. vaginatum* projection cover was over 100% (Fig. 1 in **IV**). In addition to strong seasonal variation, the leaf area increased with NO_3^- addition (Fig. 1 in **IV**). With the 10000x addition of NO_3^- the *Eriophorum vaginatum* cover increased from initial 10% to 40% and from 70% to 100% from the beginning to the peak of season.

With increasing amounts of NO_3^- relatively less was used. The same phenomenon was observed regardless of the abundance of *E. vaginatum* (Table 2 in **IV**). The surplus amount of NO_3^- was the larger the lower was the abundance of *E. vaginatum* (Table 2 in **IV**).

The NO_3−N that was not used by denitrifying microbes varied from 0.5 mg m^{-2} d^{-1} in the plot with initial 10% cover of *E. vaginatum* in prevailing NO_3^- conditions to 73 mg NO_3−N m^{-2} d^{-1} in the plot with initial cover of 70%, and with the highest NO_3^- addition (Fig. 2 in **IV**).

Variation between N_2O fluxes was large, varying from 0.1 to 385 mg m^{-2} d^{-1} (Fig. 3 in **IV**), and they were highest in early summer (Fig. 3 in **IV**) before the leaf area of *E. vaginatum* had risen to its maximum (Fig. 1 in **IV**). In the simulation with the model (Eq. 1 in **IV**), the N_2O fluxes decreased and approached asymptotically zero with increasing *E. vaginatum* leaf area (Fig. 4 in **IV**). However, denitrification appeared to saturate even with high availability of NO_3^- and without the presence of *E. vaginatum* (Fig. 4 in **IV**), but the saturation seemed to be slower than with competition by *E. vaginatum* (Fig. 4 in **IV**).

5 Discussion

5.1 Restored peatland buffer removed both N and P effectively

Only ca. 0.5% of added NO_3^- and only ca. 7% of added PO_4^{3-} was leached through the buffer during the period 1999−2001. However, the concentration of PO_4^{3-} in soil water and outflow water were high still in 2000-2001, indicating that some of the added P may have leached from the buffer area after 2001 (the last study year). Removal percentages based on a relatively short-term study as the present may thus overestimate the real removal. Thus, it is possible that P leaching from the area will increase in the future, although P leaching during the period 1999−2001 (Figs. 3 and 4) was much lower than the leaching from restored peatlands reported in e.g. Sallantaus *et al.* (2003). In addition, the constructed peatland buffer is quite large (ca. 15−25% of the catchment area) in relation to its estimated water catchment area. If the buffer had been smaller, the N and especially P retention effectiveness might also have been weaker.

The results showed that especially the added NO_3^- was mainly retained in the upper experimental area of ca. 0.2 ha (Figs. 5 and 6), whereas added PO_4^{3-} , K and Ca spread out in a much larger area, over 0.5 ha (Figs. 5−8). Thus, to achieve high N removal from through-flow waters, the required peatland buffer area may probably be much smaller than that required for P.

5.2 Processes leading to N and P removal

5.2.1 Plant biomass and nutrient retention

Nutrient retention in the vegetation is a biochemical process. Nitrogen is stored in the plant biomass mainly as amino-acids, eg. arginine, glutamine and asparagine, and proteins and nucleic acids are also involved to a lesser extent (Chapin *et al*., 1986). Phosphorus is stored mainly as soluble, organic P-compounds, such as phospholipids (Chapin *et al*., 1986). Nutrients are chemically transformed and stored mainly during autumn and winter (Chapin *et al*., 1986).

Plants growing in nutrient poor ecosystems have adapted to these conditions by having a large root and storage organ biomass and effective nutrient retention strategies (Aerts and Chapin, 2000). Species with these traits absorb nutrients in excess of their immediate growth requirements during high nutrient availability, and these reserves are then used to support growth when external nutrients are not available for plant uptake (Chapin, 1980).

Efficient nutrient retention in restored peatland buffers, especially in restored peat cut-away areas, may be explained by the vegetation-free space (Heikkilä and Lindholm, 1997; Komulainen *et al.,* 1998, 1999), which is rapidly colonised by opportunistic peatland plant species, i.e. cottongrass, sedges, Sphagna and ruderal herbs, such as *Epilobium angustifolium* and *E. adenocaulon* (Table 2 in **I**). However, the luxurious growth of ruderal herb species will probably be quite short-lived after the nutrient pulse, while the life-span and thus nutrient retention time of *E. vaginatum*, and also of sedges and Sphagna, will be longer.

Dead below-ground plant mass formed the major part of the total biomass, and total N and total P stores in all areas (Table 2 in **I**), similarly to eg. Jonasson (1982), Huttunen *et al.* (1996) and Hobbie and Chapin (1998). The high amounts of dead roots will form a very long-term nutrient storage in the peat (Mäkilä, 1994; Table 2 in

I). However, N and P are probably relocated from dead and dying organs (especially roots) to living ones, thus decreasing the N and P storage of the dead roots.

Cottongrass appears to be the key plant in the retention of N and P from throughflowing water in a restored peatland buffer, and the most responsive organs to nutrient retention seem to include the principal biomass and nutrient storage organs, i.e. the stems and leaf sheaths and roots (Table 2 in **I**).

Vegetation seems to be the most effective assimilator of N from throughflowing water. The stores of N in the long-lived plant components, and to a lesser degree those of P, are significant factors also in the long-term retention of N and P.

5.2.2 Gaseous N loss

Evidence has been found for the occurrence of both nitrification and denitrification in peat soils (Focht and Verstraete, 1977; Regina *et al.,* 1996). However, conditions in anaerobic nutrient rich peat are favourable especially for denitrification (Avnimelech, 1971). Furthermore, many denitrifiers are acid tolerant, and thus denitrification can occur also in quite low pH (Avnimelech, 1971). Nitrogen addition in this study was given as NO_3^- and water table levels in the rewetted site were relatively high, creating anaerobic NO_3^- rich conditions below the water table level (**II**). Thus, denitrification presumably produced the major share of the high N_2O fluxes in this study (**II**).

Although C_2H_2 inhibition technique is well established (Tiedje *et al.*, 1989), problems exist (Knowles, 1990). The assumption that C_2H_2 inhibits N_2O-reductase completely may not always be correct. When soils are waterlogged or compacted, C_2H_2 may not diffuse to all sites with denitrifying microbes (Malone *et al.*, 1998). Thus, much more accurate methods for measuring N_2O fluxes have been constructed, e.g. He−O_2 method (Butterbach-Bahl *et al.*, 2002). However, in this method the N_2O fluxes cannot be measured in field conditions. Because field measurements are essential for input−output studies, the He−O_2 method is thus not suitable for this study.

The N_2O fluxes in this study were on average a little higher than those from other boreal peatlands, i.e. from ca. 100−2000 μg m^{-2} d^{-1} in unfertilised plots to ca. 400−12000 μg m^{-2} d^{-1} in strongly N fertilised plots (**II**). Regina *et al.* (1996) reported small N_2O fluxes in pristine mires and usually clearly higher N_2O fluxes in drained peatlands (aerobic conditions) in central Finland. In drained peatlands N_2O was probably produced mainly by nitrification (Regina *et al.* 1996). In this study, high gaseous N losses were observed in high water table level and consequently anaerobic conditions (**II**), produced probably mainly by denitrification. Thus, these contradictory results indicate that the importance of the N_2O formation pathway (nitrification vs denitrification) in the determination of N_2O flux magnitudes is low. Instead, it seems that more important is how much inorganic N is present in the soil water for nitrifiers/denitrifiers.

Measurements of N_2O production in peat soils during winter period are limited. For instance, Flessa *et al.*, (1995) found up to 46% of the annual N_2O fluxes during December and January for soils in southern Germany. Maljanen *et al.*, (2003) reported that N_2O fluxes decreased towards autumn, but increased again in winter when the air temperature was below 0ºC and the soil was covered with snow in eastern Finland. In this study the N_2O fluxes during winter were 33-36% of the annual N_2O fluxes, and thus significantly lower than in the growing season, but nevertheless remarkable (**II**). The significant decrease in N_2O production in winter was mainly due to the decrease in soil temperatures (Figs 2 and 3 in **II**).

High water table levels and the rise of water to the soil layers with fresh organic material, and releasing N from dying and decomposing plants during autumn and winter may favour denitrification (Jacks *et al.*, 1994), which is shown in raised N_2O emission levels during autumn (Maljanen *et al*., 2003). Quite high N_2O fluxes were also observed during winter also in this study, and thus the long winter period is important in the total annual gaseous N loss in boreal peatlands.

The results obtained in this study show that the gaseous N production in peat soil can be regarded as a N loss mechanism for peatland buffer, but it is a very short-term process, lasting only the duration of the N pulse. However, it removes N from soil water effectively just at the time when the N pulse is at its highest.

Restored peatland buffers may emit considerable amounts of N_2O into the atmosphere, thus enhancing the greenhouse effect and the depletion of stratospheric ozone, especially if there are large amounts of NO_3^- present in the soil water. However, the area of drained peatlands restored for water protection purposes will remain small compared to the whole peatland area in northern boreal zones, and thus the total increase of N_2O emissions will be low.

5.2.3 Nutrient retention in microbial biomass

Direct estimation of microbial C, N and P was made possible with the development of the fumigation extraction method (Brookes *et al.,* 1982; Brookes *et al.,* 1985; Vance *et al.,* 1987). The k_{EC}, k_{EN} and k_{EP} factors are used to correct for the incomplete release and extraction of microbial C, N and P following $CHCl_3$ fumigation and they form an important determinant of the precision of measurements using this method (Joergensen, 1996).

Joergensen and Scheu (1999) have also reported that the addition of C, N and P increased the amounts of microbial C, N and P especially in the L-horizon of a claysoil in Germany. Thus, if carbon and nutrients are available microbes increase their biomass, together with N and P storage both in mineral and peat soils.

In this study microbial C values (Fig. 2 in **III**) were rather similar to the values reported by Kaiser *et al.* (1995) in an arable luvisol soil in Germany and by Tessier *et al.* (1998) in an agricultural humic gleysol in Canada. However, the soils in these studies differed much from this study, and the soil pH was probably much higher. The microbial C values in this study were much lower than the values reported by Brake *et al.* (1999) in the *Sphagnum*-peat of a drained grassland and by Baum et al. (2003) in a rewetted *Carex*-peat in Germany, possibly because of a lower pH in this study. Also the microbial N and P values in this study were much lower than the values by Brake *et al.* (1999) and Baum *et al.* (2003).

The main flourishing bacteria groups in nitrate (NO_3^-) rich conditions are denitrifying bacteria (e.g. Focht and Verstraete, 1977; Jenkinson and Ladd, 1981). In this study, added N was in the form of NO_3^- and we observed a significant increase in N_2O emissions in the upper experimental area soon after the N and P addition had been started in 1999 (**II**). Thus, probably a significant part of the increased microbial biomass (**III**) consists of denitrifying bacteria.

The soil microbial community in low pH soils grows slowly compared to life-spans of microbes generally (Alexander, 1961; Gyllenberg and Eklund, 1974). Bacterial cell division rates from one per 9.3 days (Bååth, 1998) to as low as one per 180 days (Jenkinson and Ladd, 1981) have been reported. Generally, in organic peat soils fungi with longer life-spans are more abundant than bacteria (Gyllenberg and

Eklund, 1974), and thus it is presumable that microbial nutrient retention may be of longer-term than in mineral soils with higher pH.

After death the cytoplasm of microbes will lyse and decompose rapidly, but the residues of cell walls will decompose more slowly (Gyllenberg and Eklund, 1974; Jenkinson and Ladd, 1981). Consequently, some N and P may still remain in the slowly decomposing residues of microbial cells and the microbial retention of N, and especially of P may be quite long-term after transient nutrient loading. In the study of Jonasson and Michelsen (1996), the retention times of N and P in the microbial biomass were 7.5 and >30 years, respectively. Since the loss of P from soil and fertilisers is the major cause of eutrophication in water bodies (Leinweber *et al*., 1999), effective and long-term microbial P retention in the constructed peatland buffer is an important factor in the prevention of P leaching in the water bodies.

5.2.4 Nutrient retention in peat matrix

The P retention capacity of peat is directly related to its Al and Fe concentrations (Kaila, 1959; Cuttle, 1983) and pH in soil water (Murrmann and Peech, 1969). Since water movement in the peat occurs mainly in the large pores, thus reducing contact surface with a large portion of the peat matrix, existing phosphorus adsorption isotherms can not usually be used as indicators for P retention (Richardson, 1985). Thus, input − output data is the only method to determine the actual retention capacity of P (Nieminen and Jarva, 1996).

In this study the peat matrix seemed to be the most important P retaining component (Fig. 9), but had no effect in the retention of added N, since the retention of NO_3−N in the peat matrix is negligible (Black, 1968). Phosphorus retention in the peat matrix is probably largely governed by the aluminium and iron phosphate formation supported by the significant positive correlations between peat P and Al and Fe concentrations in each year 1998-2000.

Also Kaila (1959) found a significant correlation for P with Al and Fe concentrations in different peat soils collected from pristine mires, and Nieminen and Jarva (1996) especially between Fe and P concentrations. Kaila (1959) found stronger correlation between Al and P concentrations than between Fe and P concentrations, but Nieminen and Jarva (1996) between Fe and P concentrations. In this study the correlations were stronger between Fe and P concentrations than between Al and P concentrations. Differences in the results between these studies could be influenced by the differencies in peat types (different peat Al and Fe contents) and land use histories of the sites (pristine mires, peatlands drained for forestry and restored peatlands). Thus, the results of this study imply, similarly to Nieminen and Jarva (1996), the lower significance of Al phosphate formation in retention of P in the peat matrix than the Fe phosphate formation.

5.2.5 Effect of *Eriophorum vaginatum* on N and P cycling in restored peatland buffers

5.2.5.1 Nutrient retention in E. vaginatum

The survival of several leaf blades and leaf stems during winter, only to die early in the growing season suggests that these serve not only as a source of carbohydrates and nutrients, but also as photosynthetic tissues, to support early spring growth of cottongrass (Shaver *et al*., 1986; **V**). The evergreen habit of cottongrass is consistent with the theory of evergreen species being the effective exploiters of infertile soils (Grime, 1977; Mark and Chapin, 1989).

The high accumulation of biomass, as well as N and P in the overwintering storage organs supports this. The rapid early growth of cottongrass in the greenhouse experiment (Fig. 4 in **V**), even though all roots were removed before planting, reveals the insignificant role of root system in the early season.

The high biomass of new photosynthetic tissues was mainly produced with recently uptaken nutrients. The maximum leaf elongation and new daughter tiller production occurred in June − August (Figs. 1 and 3 in **V**), concurrently with the highest nutrient uptake (Fig. 6 in **V**) and increased with nutrient availability.

In spite of the moderately increased leaf lengths and the number of cohorts (Fig. 1) the high nutrient input was mainly allocated to the production of new daughter tillers (Fig. 2 in **V**). This strategy in allocation was similarly observed in Alaskan tussock tundra (Shaver *et al*., 1986).

Towards the end of the growing season, additional nutrient uptake was stored in stems and leaf sheaths to support the start of the next season's production (Fig. 4 in **V**), similarly to Alaska (Shaver *et al.*, 1986). Most cottongrass tissues die during winter (Wein, 1973), except the storage organs and part of the leaves (Fig. 5 in **V**), and at the beginning of the next growing season previous years living root biomass will form the dead root mass (Wein, 1973). In spite of effective relocation of nutrients, a part will remain in the dying biomass (Shaver and Chapin, 1995). Macroscopically identifiable residues of roots and leaf sheaths found in large quantities in peats with ages of several thousands of years (Mäkilä, 1994) implies that the annually increasing mass of dead roots may form a major long-term sink for nutrients. The results obtained in this study indicate that cottongrass allocates biomass and nutrients in the slowly decomposing storage organs (stems and leaf sheaths and roots) proportionally more than in the rapidly decomposing organs (leaf blades).

Although cottongrass is capable of thriving in nutrient poor habitats it has an adaptation to luxury nutrient uptake and biomass accumulation in conditions with excessive nutrient supply. The slow decomposition of annually increasing mass of dead storage organs forms a long-term sink for nutrients, and thus cottongrass may play an essential role in the long-term nutrient retention of restored peatland buffers.

5.2.5.2 Competition for NO_3^- between E. vaginatum and microbes

Conditions in anaerobic nutrient rich peat are favourable for denitrification (Avnimelech, 1971; **II**; **IV**), which was seen as high N_2O fluxes from peat surfaces without vegetation with high available NO_3^- (Fig. 3 in **IV**). The large variation between N_2O fluxes (Fig. 3) was mainly due to varying NO_3^- concentrations in soil water, controlled by the NO_3^- addition and the abundance of cottongrass (Table 2 in **IV**). Thus, cottongrass appears to be a superior competitor for NO_3^- with denitrifying microbes, which have often been regarded as stronger competitors for inorganic N (Johnson, 1992; Kaye and Hart, 1997). However, one possible explanation of the decrease of N_2O fluxes in the presence of cottongrass in addition to resource competition is the increasing reduction of N_2O to N_2 due to enhanced rhizosphere activity (Mander *et al.*, 2003). Our findings give support to the results of Korsaeth *et al.* (2001), which showed that plants may be stronger competitors for inorganic N. In their model plant N uptake was described as a linear function and microbial N use followed the Michaelis–Menten kinetics, from the microbial point of view similarly to our model.

However, the competition potential of plants is obviously linked to their growth and biomass production rates. Ecosystems where micro-organisms have shown to be

stronger competitors than plants seem to be situated mostly in warm and dry regions, and dominated by slow-growing plants with low nutrient uptake efficiency (Schimel *et al.*, 1989; Hart *et al*., 1992; Johnson, 1992).

Instead, rapidly growing herbaceous vegetation with high nutrient uptake efficiency in strongly N fertilised conditions appears to be stronger competitor for inorganic N than microbes (Wang and Bakken, 1997; Korsaeth *et al*., 2001). According to our study, rapidly growing plants may be stronger competitor also in wet, peat accumulating ecosystems, because the duration of N-input may affect the N retention capacity of plants (Johnson, 1992). In addition, outside the growing season, microbes utilise the available N released from dying and decomposing annual parts of plants, which is shown in raised N_2O emission levels (Maljanen *et al.*, 2003).

Conclusively, our results indicate that rapidly growing vegetation is a major control of N_2O fluxes in sedge dominated peatlands during the growing season reducing the amount of available NO_3^- for denitrification and decreasing the N_2O emissions from these ecosystems.

5.3 Validity of the experimental design

Choosing the number and size of both experimental site(s) and sample plots is a trade-off between increased accuracy and reliability of estimates and increased effort and costs. This study consisted of only one experimental site, and this may hamper the generalisation and upscaling of the results. However, the indentification and quantification of ecological processes connected to the nutrient removal was the main aim of this study, and this aim can be best achieved by using one intensively investigated study site. The nutrient removal capacity varies probably largely depending on the size of the buffer, soil type, moisture and topography, but the nutrient retention processes of the "typical" restored tall sedge pine fens can be similar to this study.

Because of the artesian discharge water from the near Vatiharju esker, it is difficult to accurately estimate the area of the catchment above the studied buffer. However, the proportion of the buffer from the catchment in the present study (15-25% on the basis of careful levelling) is probably much higher than for the buffer areas used generally in practical forestry. As the retention of N and P is likely to be strongly related to the size of the buffer, significantly lower removal rates as presented here may be achieved by the buffers used in practical forestry.

One possible source of error in the present study is that some exchange of nutrients probably occurs between the upper and lower treatment areas and the control area. However, the effect of this exchange on N and P cycling is probably minimal compared with the very high differences in soil water NO_3^- and PO_4^{3-} concentrations between the areas as shown in Figs. 5 and 6.

6 Conclusions

The national water protection programme aims at decreasing the nutrient loads from forested areas until 2005 by 50 % from the level of 1993. Thus, in the future, the control of the detrimental effects of forestry operations on water bodies will become increasingly important. One of the means in controlling nutrient leaching is to restore sections of drained peatlands for creating buffer zones between forest land and water bodies. The results from an intensively monitored restored peatland buffer in central Finland showed that restored peatland buffers may significantly decrease N and P leaching to water courses. The long-term nutrient retention rates of restored peatland

buffers may necessarily not be particularly high, but in the case of suddenly increased transient nutrient loadings, retention may be substantial. However, because this study covered only one study site and only a three years' monitoring period a larger study with several sites and longer monitoring period is needed. From the viewpoint of ecosystem functioning, this study provides a more accurate picture of the retention processes in the restored peatland buffers than much of the earlier research, which was mainly based on "black-box" studies with no investigations on the ecological processes.

As regards forestry operations in forested peatlands, this study provides a theoretical basis for the development of buffer constructing methods. Potentially each drainage area should include a restored buffer part through which outgoing water both from the drainage area and from the surrounding upland forest catchment would be filtered.

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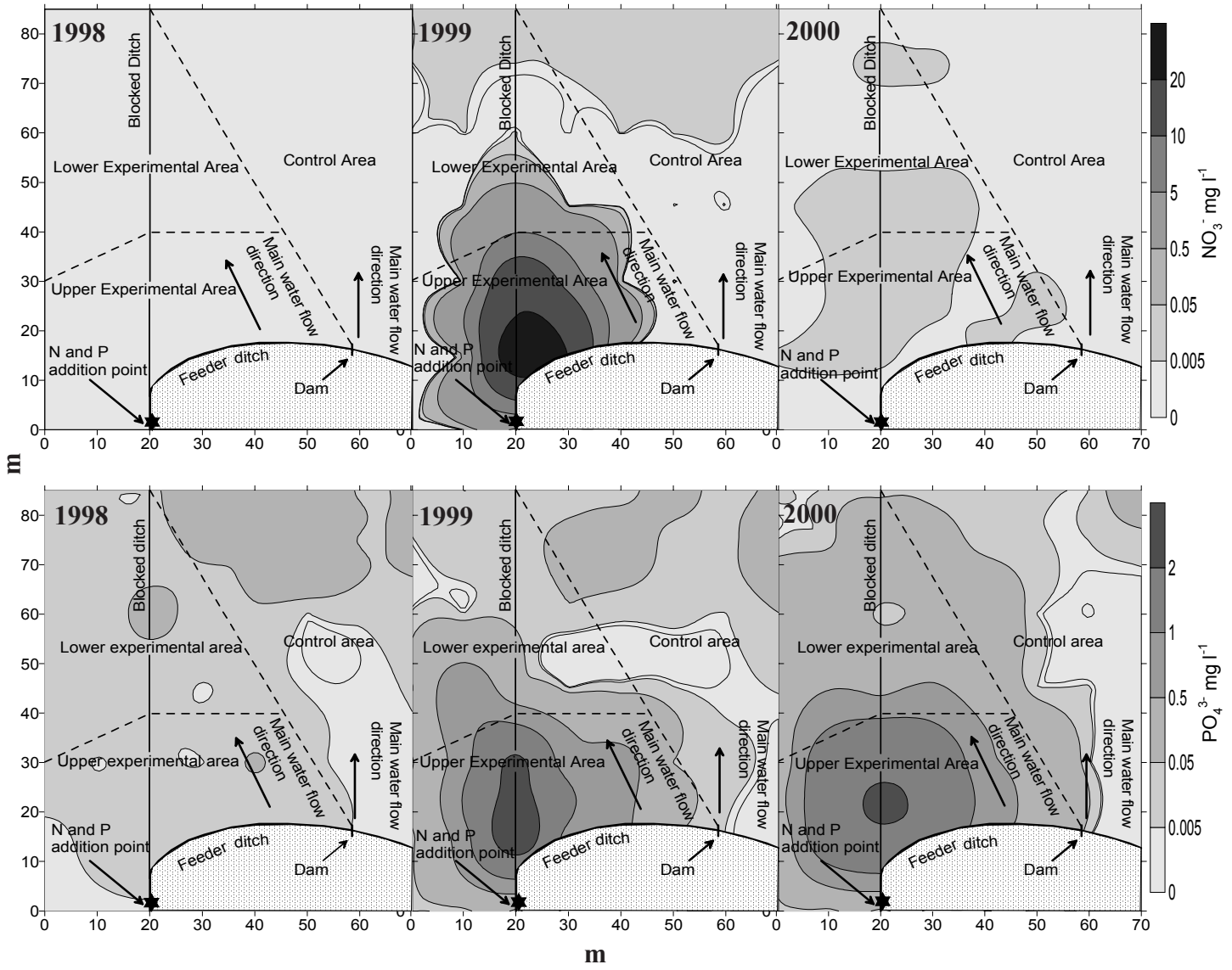

1998
1999
2000
Blocked Ditch
Lower Experimental Area
Control Area
Upper Experimental Area
Main water flow direction
N and P addition point
Feeder ditch
Dam
NO_3^- mg l^{-1}
20
10
5
0.5
0.05
0.005
0
m

1998
1999
2000
Blocked ditch
Lower experimental area
Control area
Upper experimental area
Main water flow direction
N and P addition point
Feeder ditch
Dam
PO_4^{3-} mg l^{-1}
2
1
0.5
0.05
0.005
0
m

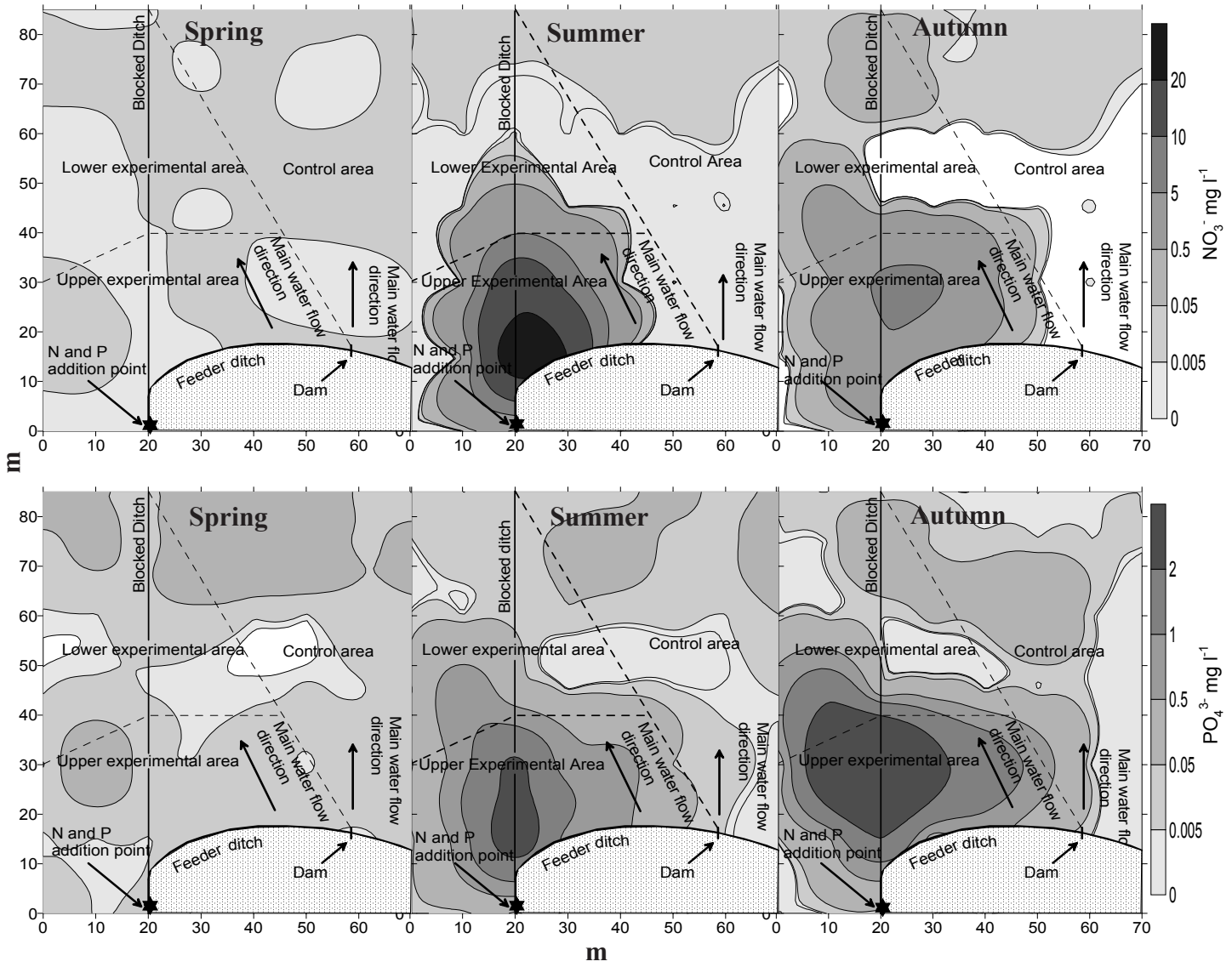
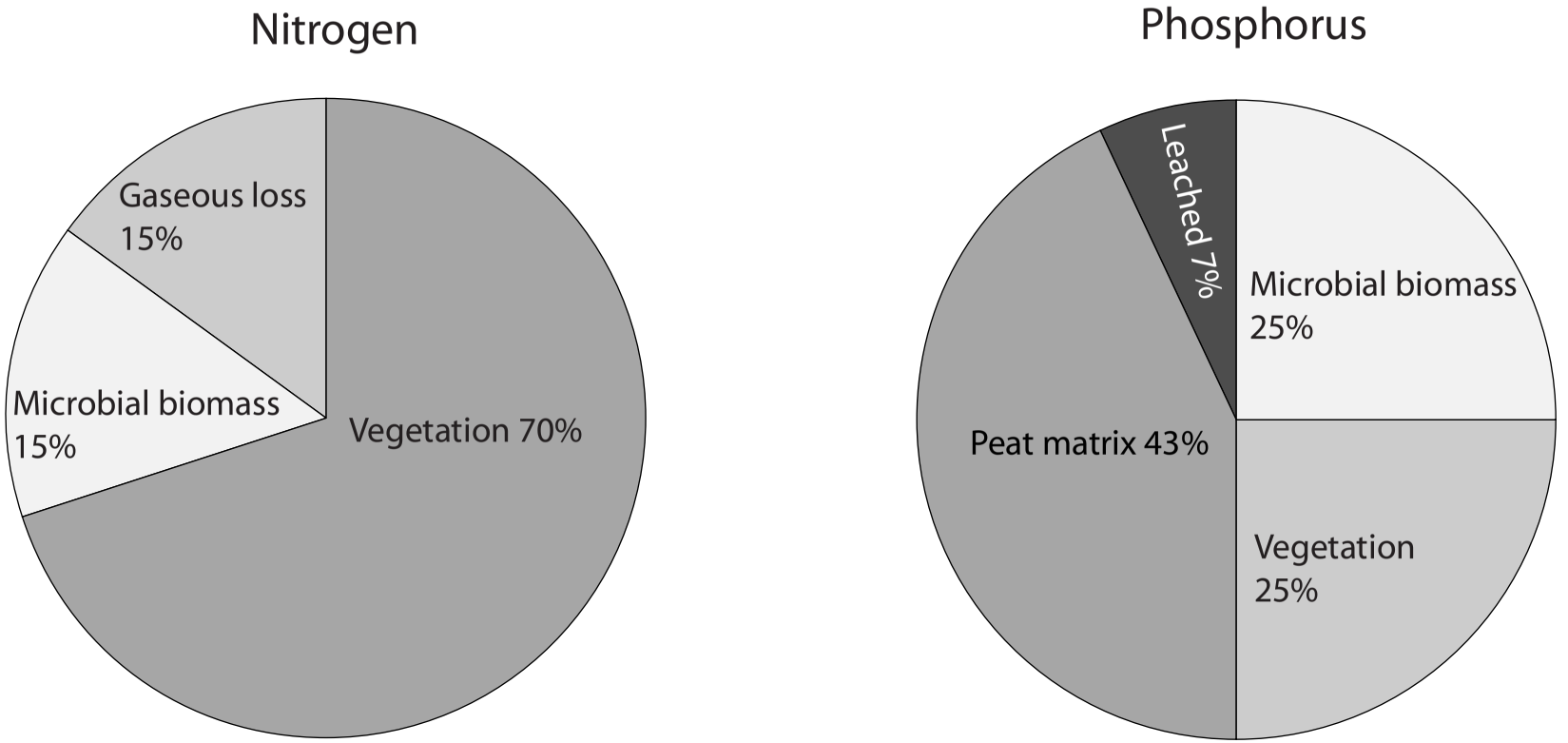
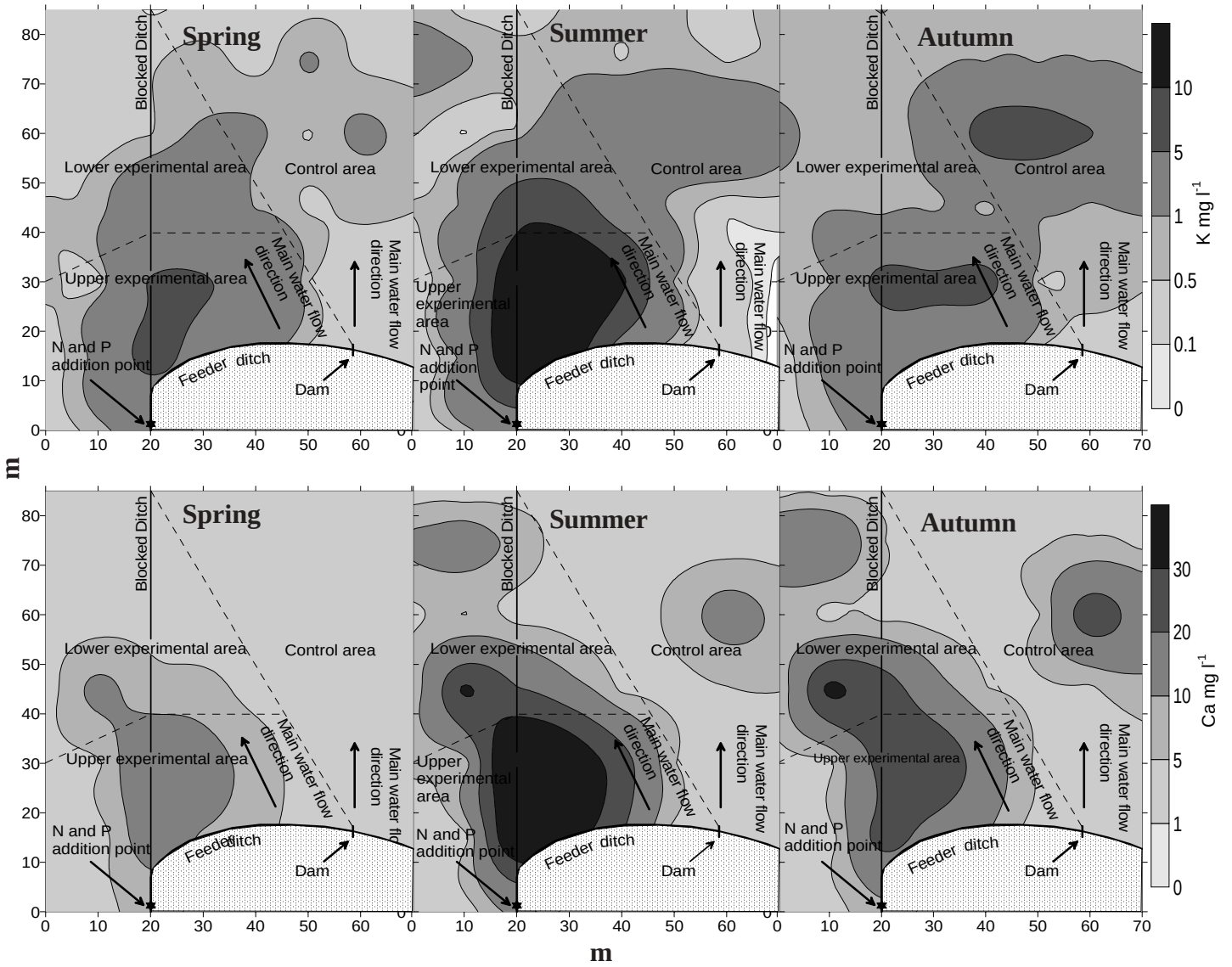

Spring
Summer
Autumn
Blocked Ditch
Lower experimental area
Control area
Upper experimental area
Main water flow direction
N and P addition point
Feeder ditch
Dam
NO_3^- mg l^{-1}
PO_4^{3-} mg l^{-1}
m

Table 1. The balance sheet of N and P load (natural and artificial), release and retention (kg) in the biological and the geochemical processes in the upper and lower experimental areas combined (U+L) and control area separately. Natural N and P load and release due to nutrient addition was calculated for the period 1999-2001. The N and P release was calculated by subtracting the natural release (release in 1998) from the measured release in 1999-2001.

U+L	Natural load	Addition	Retention				Release from addition
			Peat matrix	Vegetation	Gaseous loss	Microbes	
NO_3-N	0.008−0.043	45.0	0	31.4	5.5	6.8	0.28
PO_4-P	0.004−0.009	15.0	6.8	3.6	0	3.6	1.03
Control	Natural load	Addition	Peat matrix	Vegetation	Gaseous loss	Microbes	
NO_3-N	0.018−0.067	0	0	4.7	1.0	0.1	0
PO_4-P	0.015−0.031	0	0.0	0.5	0	-0.6	0


Nitrogen
Gaseous loss
15%
Microbial biomass
15%
Vegetation 70%
Phosphorus
Leached 7%
Microbial biomass
25%
Peat matrix 43%
Vegetation
25%


Spring
Summer
Autumn
Blocked Ditch
Lower experimental area
Control area
Upper experimental area
Upper experimental area
Main water flow direction
N and P addition point
Feeder ditch
Dam
K mg l-1
10
5
1
0.5
0.1
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Ca mg l-1
30
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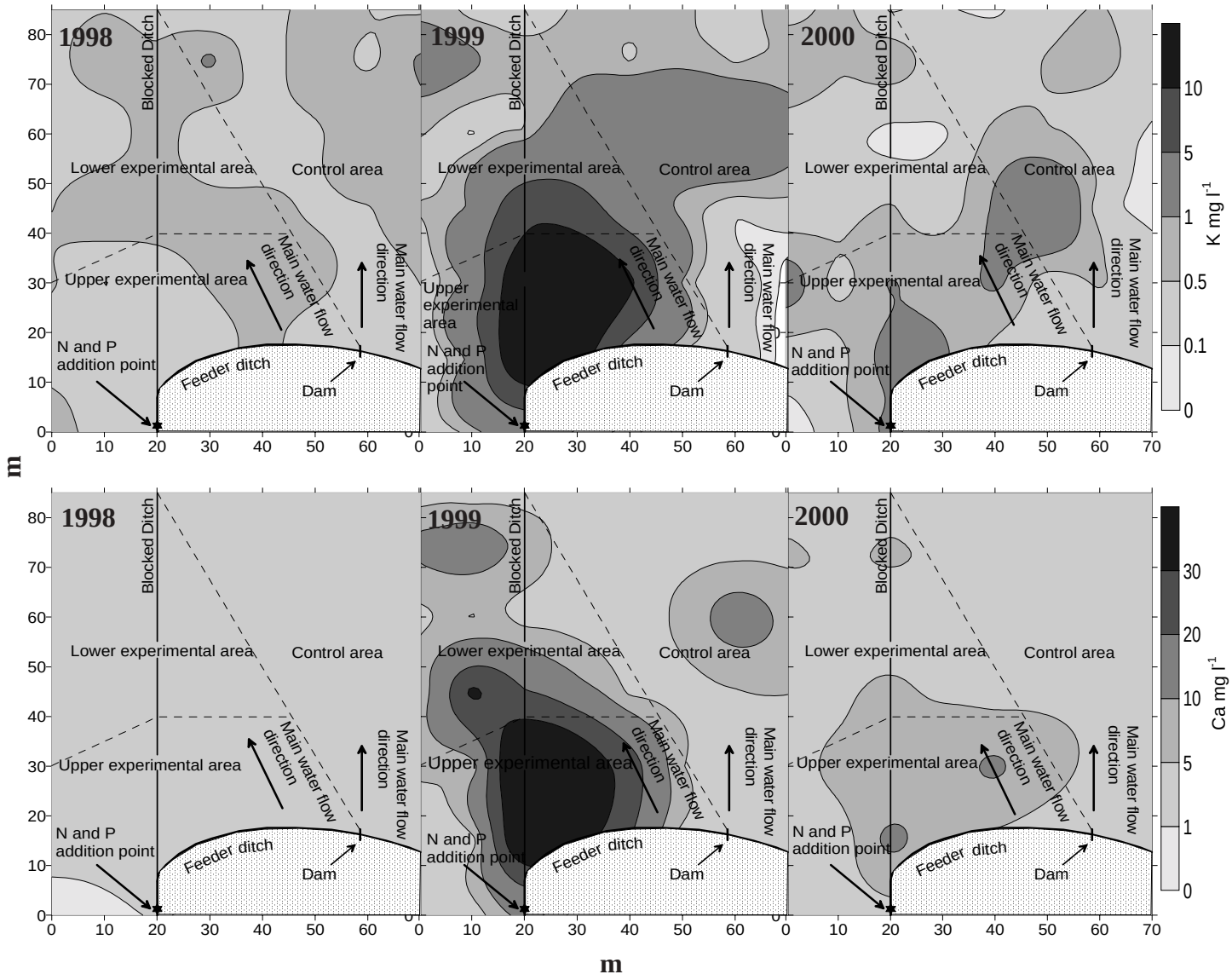
1998
1999
2000
Blocked Ditch
Lower experimental area
Control area
Upper experimental area
Upper experimental area
Main water flow direction
N and P addition point
Feeder ditch
Dam
K mg l-1
10
5
1
0.5
0.1
0
Ca mg l-1
30
20
10
5
1
0
m
m

Table 2. Average peat Al and Fe concentrations ± SE (mg g^{-1}) in the experimental areas during 1998-2000.

	1998		**1999**		**2000**	
	Al	Fe	Al	Fe	Al	Fe
Upper	0.755± 0.049	2.160± 0.222	0.896± 0.103	2.060± 0.255	0.814± 0.089	2.137± 0.177
Lower	0.861± 0.054	2.380± 0.239	0.613± 0.064	2.298± 0.404	0.801± 0.037	2.363± 0.158
Control	0.726± 0.049	2.265± 0.246	0.816± 0.097	2.436± 0.397	0.746± 0.065	2.410± 0.324