

Floods can cause large interannual differences in littoral net ecosystem productivity

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Abstract

Littoral wetlands comprise a terrestrial to aquatic continuum along which carbon dioxide is exchanged with the atmosphere and organic carbon is transferred to lakes. Net ecosystem productivity—the difference between atmospheric CO₂ uptake and total ecosystem respiration—in these shore areas depends partly on the extent and duration of spring flooding. Ecosystem-atmosphere CO₂ fluxes were studied at a boreal lake in Finland to analyze how flooding affects the dynamics of littoral net ecosystem productivity. Two shore transects with different hydrological conditions and vegetation distributions were studied during consecutive ice-free periods with contrasting flooding patterns. Net ecosystem productivity in different vegetation zones did not respond consistently to extended flooding; the response depended on the phenology of plant emergence during the flood and on the decrease in the water level after flooding. The decrease in the water level was steeper in silt-mud sediment than in fen peat. With an exceptionally high water level relative to the height of the vegetation, net ecosystem productivity decreased by 50–100% (net loss, 0.4–7.4 mol m⁻² of CO₂ during the wetter open-water period). However, the wetter season could also have a 60–140% higher net ecosystem productivity (net CO₂ gain of 0.7 mol m⁻² to net loss of 6.8 mol m⁻²) because of the decreased decomposition rate. An extended flooding period greatly reduces the amount of litter produced in a specific year. In both flooding patterns, the littoral zone was an overall net CO₂ emitter, but the large variation in the decomposition rate suggests that there are differences in the load of organic matter from the littoral to the pelagic zone.

Carbon cycling is increasingly known in several terrestrial and aquatic ecosystems (e.g., Molau et al. 1999). Our study was carried out at the interface of boreal forest and lake ecosystems, on littoral wetlands, and thus supplements the knowledge about carbon exchange in a continuum from a terrestrial to an aquatic ecosystem. The dynamics of primary production and decomposition in these transition zones are potentially large but are still poorly known (Brix et al. 2001).

In boreal lakes, the most important event involving an input of organic carbon and nutrients from the catchment is the spring flood after snow melt (Kortelainen et al. 1997). At that time, water runoff from the catchment increases, and the water level in the lake and adjacent littoral wetland rises. If the topography is flat, then the inundated area can even

be larger than the lake (e.g., Wetzel 1990). In shallow boreal lakes, the variation in the water level within the space of 1 yr and between years can be >1 m, and the duration of flooding on a littoral site therefore also varies by several weeks during the growing season.

The water level both directly and indirectly affects ecosystem CO₂ exchange, the CO₂ influx from the atmosphere (gross photosynthesis, P_g), and the efflux to the atmosphere (ecosystem respiration, R_{tot}). The water level primarily regulates the duration of oxic and anoxic conditions in the sediment and thus directly affects the proportion of soil respiration in ecosystem CO₂ efflux (e.g., Billings et al. 1982; Moore and Knowles 1989). Littoral plants need to tolerate flooding and the shortage of oxygen in the rhizosphere to survive. Thus, oxygen transport is mediated via aerenchyma to submerged organs, and the elongation of shoots ensures photosynthesis in the air (Blom and Voosenek 1996). Littoral macrophyte and algal primary production contributes fresh, easily degradable organic matter to the lake ecosystem. The autochthonous dissolved organic carbon (DOC) from littoral wetlands has been suggested to be the largest continuous

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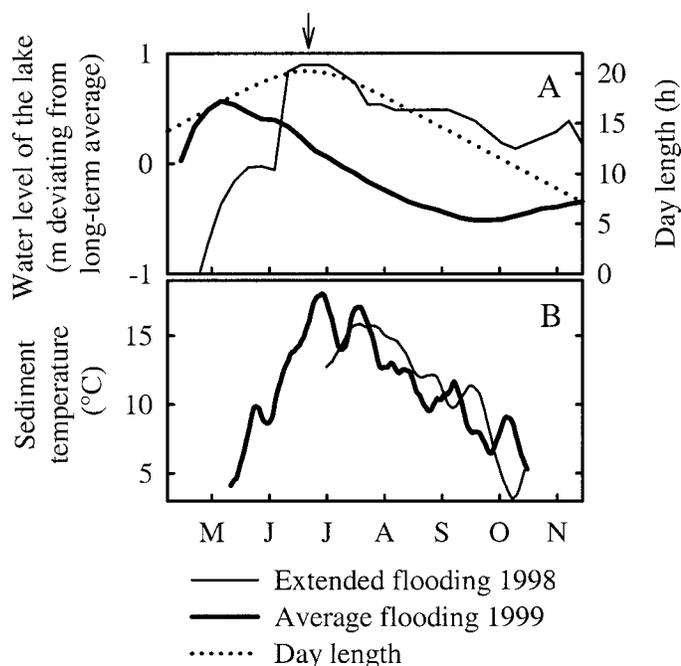


Fig. 1. (A) Flooding regimes at Lake Mekrijärvi during the study seasons: extended period of flooding 1998 and near-average flooding 1999. The water level of the lake and day length are shown. Extended flooding coincided with the phase of highest potential photosynthetic activity during midsummer (arrow). (B) The 7-d running average of mean daily temperature of the sediment surface at the fen during the seasons.

load of DOC to lake ecosystems (Wetzel 1992). Part of the allochthonous and autochthonous carbon is released as CO₂ back to the atmosphere. The difference between the influx and efflux of atmospheric CO₂ determines the instantaneous net ecosystem CO₂ exchange (NEE). NEE over the growing season is also considered to be net ecosystem productivity (Bubier et al. 1999).

The aim of the present study was to analyze how the duration and timing of flooding affect net ecosystem productivity in the lake littoral. Two years with contrasting flooding patterns allowed us to compare CO₂ fluxes, gross photosynthesis, and ecosystem respiration during a season with prolonged flooding and a season with near-average flooding. A longer period of inundation may reduce seasonal primary production and, thus, the supply of fresh organic matter for decomposers. However, as the result of a high water level, the overall CO₂ release from the decomposition of organic matter harbored in sediments would also be suppressed and more old litter preserved compared with a drier year. Because plant phenology is controlled by the length of the day, an extended period of flooding would coincide with the most favorable midsummer period for photosynthesis (Fig. 1). We hypothesized that the timing of spring flooding would be critical to vegetation development but not to littoral CO₂ release in decomposition because the sediment temperature is still high even later in the season. Thus, extended flooding would result in a greater gaseous net loss of carbon from the littoral than that during near-average flooding.

Materials and methods

Study site—The study was carried out in 1998–1999 at the polyhumic, mesoeutrophic Lake Mekrijärvi, Ilomantsi (62°45'N, 31°00'E, 144.5 m asl) in eastern Finland. The lake is a shallow upstream lake with an area of 12 km², a mean depth of 1.7 m, and maximum depth of 3 m. The catchment of the lake (4000 km²) consists mainly of peatlands and forests. Ice covers the lake from early November to early May, and the spring flood has usually drawn down by midsummer.

The study years had contrasting weather conditions and flooding regimes (Fig. 1). In 1998, the precipitation was 1.2 times the 30-yr average for the region (669 mm, 1971–2000; Drebs et al. 2002), and the water level was one of the highest in 20-yr records. In 1999, the precipitation was 0.9 times the 30-yr average, and the water level in Lake Mekrijärvi was close to the long-term average. The difference in the median water level of the open water period was 66 cm between the years.

Two study transects (60–85 m long) were established in the flooded littoral (i.e., eulittoral) of Lake Mekrijärvi from the upper limit of the flood to the lower limit of emergent vegetation (Fig. 2), one on a marsh and the other on a lacustrine fen. The sites were chosen for their well-developed zonation in sedge-dominated vegetation characteristic to the lake and common to wetlands in the boreal region. In these types of lacustrine ecosystem, the vegetation resembles that of mires, but the lake regulates the hydrology of the sites. At the marsh site, the transect covered a moisture gradient ranging from the margin of a pine forest to marsh dominated by *Carex aquatilis* Wahlenb. At the fen site, the drier sedge fen was dominated by *C. lasiocarpa* Ehrh. and *Molinia caerulea* (L.) Moench, and the most frequently inundated fen was characterized by *Comarum palustre* L. At both sites, the moss cover consisted mainly of *Sphagnum* species.

Measurement of CO₂ fluxes—To capture the spatial variability of ecosystem-atmosphere CO₂ exchange in the littoral zone, 14–16 permanent plots were established for chamber measurement along each transect during spring 1998. To minimize disturbance during the measurements, boardwalks were built beside the sample plots. Measurement collars (60 × 60 cm) were adjusted according to the fluctuating water level. Later, when the water table had fallen below the soil surface, the collars were inserted into the sediment to a depth of 20 cm. Gas fluxes were measured once or twice a week during 2 July–8 October 1998 and during 19 May–11 October 1999. Most of the measurements were made in daytime, but day-round measurements were carried out during 14–18 June and 16–20 August 1999.

Ecosystem-atmosphere CO₂ exchange was measured using paired closed chambers fitted on preinstalled collars (Alm et al. 1997). The instant NEE was measured under prevailing weather conditions with a vented and thermoregulated ($\pm 1^\circ\text{C}$ outside air temperature) polycarbonate chamber, and R_{tot} was measured with an opaque chamber. The CO₂ concentration in the chamber headspace (volume 47–317 liters) was monitored every 30 s for 150–240 s with a portable infrared gas analyzer (ADC, LCA-2; Analytical Development) equipped with a pump (suction from the headspace,

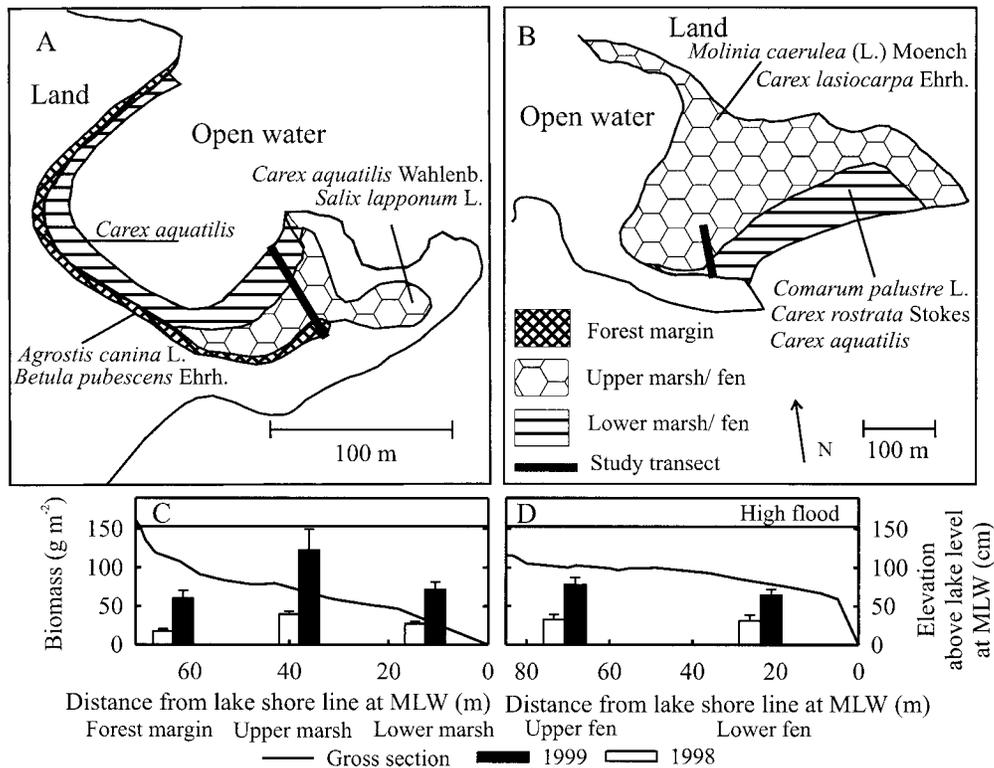


Fig. 2. Littoral study sites at the (A) marsh and (B) fen. The littoral zonation, the dominant species for each subzone and the study transects are shown. Mapping of the study area by Juutinen et al. (2003). Elevation profiles of the (C) marsh and (D) fen transects and average above-ground vascular plant biomass in August 1998 and 1999. High flood: the water level of the lake during the highest flood in 1998. MLW: mean low water.

150 ml min⁻¹). The air drawn by the analyzer was compensated with outside air through a pressure equilibration tube (diameter 8 mm, length 3 m). Prevailing photosynthetically active radiation (PAR) and air and sediment temperature (surface and -2, -5, and -10 cm) were recorded simultaneously. Gas fluxes were calculated from the linear change ($r^2 \geq 0.90$) in CO₂ concentration during the measurement period. Individual measurements were also rejected if the coefficient of variation in irradiance was >10% during the daytime measurement.

Environmental conditions were recorded hourly in May–October with a weather station located within 3 km of the sites (GroWeather; Davis Instruments). In addition, the surface temperature of the sediment in each subzone (*see below*) was recorded hourly during the open-water period using data loggers (Hobo; Onset Computer). The water level of the lake was monitored daily by means of a scale on a fixed pole and the water level on littoral sites in groundwater wells located next to each measurement plot.

Vegetation and sediment analyses—The plant species composition and percentage cover in each collar were determined during late July in both years. During the growing season, the number and the height of shoots in the collars were monitored every 2–4 weeks. In late August, the above-ground vascular plant biomass was harvested on 5–11 randomly distributed plots of 0.25 m² in each subzone. The

living plant material was sorted by species, dried at 105°C, and weighed. Subsamples of 50 shoots of each dominant sedge and graminoid species (mean cover >1%) were used for modeling the shoot mass in relation to height. These equations and the mean masses of other species were used in estimating the above-ground biomass in the collars. Interannual differences in above-ground vascular plant biomass in the collars were tested with the Wilcoxon paired-sample test (Zar 1999).

In late August 1998, moss biomass was sampled from a subplot of 0.025 m² on three to four of the plots harvested for determining the vascular plant biomass in each subzone. In 1999, mosses were sampled from the upper, middle, and lower parts of each transect in three replicates for determining the water content in July and October. The samples, sorted by species, were immediately weighed, dried for 24 h at 70°C, and weighed again to determine the fresh mass and dry mass. The water content (% of dry mass) of the mosses was used as an indicator of drought stress.

In late August 1998, below-ground plant biomass was sampled from three of the plots harvested for determining the above-ground biomass and in each subzone, except for the wettest marsh. Sediment samples (surface area 7.5 × 7.5 cm) were cored to a depth of 30 cm with a box sampler. Living rhizomes and roots were sorted from the sediment, dried at 70°C, and weighed. The average vascular above-ground:below-ground ratio of the given subzone was used

to estimate the below-ground biomass in each collar. In each subzone, additional sediment samples were cored for soil analyses. The organic matter content was determined as the loss in weight on ignition (LOI), and carbon and nitrogen content were analyzed with an elemental analyzer (CHN-S/O 1106 m-E; Carlo Erba Strumentazione).

Plant species composition was related to environmental variables by means of canonical correspondence analysis (CCA; ter Braak 1986) to characterize subzones in the continuum of vegetation and moisture in the study sites. The environmental variables used were the duration of flooding in the year with a near-average flood (in days from the start of the 1999 growing season), soil organic matter content (LOI), and the carbon:nitrogen ratio in the sediment. Scores for the plots were derived from weighted mean scores for the species. The significance of the axes was tested with the Monte Carlo test (PC-Ord; MjM Software).

Models for CO₂ fluxes—The seasonal CO₂ exchange was integrated on the basis of hourly environmental data using the statistical relationship between the instantaneous flux rate and environmental factors (Alm et al. 1997). For each subzone separately, a subsample of 70% of the data was randomly selected for the regression modeling, and the remaining 30% was used for validation of the models. Two-tailed Pearson correlations between the predicted and validation data were calculated.

To take into account the change in the photosynthetic activity of plants during the growing season, the 3-week running average (13 d before and 7 d after) of the mean daily air temperature (T_{ave}) was used as a technical variable to describe the phase of vegetation development. The values of two growing seasons were standardized to a scale from 0 to 1 by dividing the daily values of T_{ave} by the maximum value ($^{\circ}\text{C } ^{\circ}\text{C}^{-1}$) of the warmer growing season, 1999.

The dependence of gross photosynthesis (P_g , $\text{mmol m}^{-2} \text{h}^{-1}$) on irradiance (I , $\mu\text{mol m}^{-2} \text{s}^{-1}$) had the form of a rectangular hyperbola with Q (asymptotic maximum, $\text{mmol m}^{-2} \text{h}^{-1}$) and k (half-saturation constant, $\mu\text{mol m}^{-2} \text{s}^{-1}$). Photosynthesis depended on T_{ave} and the depth of the water table (WT , cm),

$$P_g = Q \times I \times T_{\text{ave}} / ((k + I) \times \{1 + \exp[-(WT - u_p)/t_p]\}) \quad (1)$$

whereas respiration (R_{tot} , $\text{mmol m}^{-2} \text{h}^{-1}$) depended on the temperature of the sediment surface (T_{surface} , $^{\circ}\text{C}$) and WT ,

$$R_{\text{tot}} = a \times \exp[b \times T_{\text{surface}}] / \{1 + \exp[-(WT - u_r)/t_r]\} \quad (2)$$

The effect of WT on photosynthesis and respiration had a sigmoid form, in which the coefficients u_p and u_r determine the depth of the water table for the fastest change in response of photosynthesis and respiration, respectively, and the coefficients t_p and t_r determine the direction of change along the gradient of the decreasing water table.

The coefficients were estimated using the nonlinear Levenberg-Marquardt technique (SPSS 10.1 for Windows), and the significance of the parameters was tested with the F -test (Edwards 1979). Because of the multiplicative form of the

models, the sensitivity of model predictions to variations in the model variables was analyzed by increasing each variable by 10%, both one at a time and all simultaneously, and then calculating the change in the estimated CO₂ flux.

The regression models for each subzone and the time series of environmental data were used to reconstruct hourly P_g and R_{tot} values for the period when the plants were emerging from the water (late June–October 1998 and May–October 1999). To take into account the variation in irradiance, hourly P_g values were calculated by averaging two influx values estimated from the mean irradiance \pm SD (Smolander 1984). The hourly net CO₂ exchange was calculated as $P_g - R_{\text{tot}}$. Before plant emergence and after senescence, the NEE was interpolated from weekly averages of measured net and total CO₂ efflux from the open-water surfaces. Missing values in the very beginning and end of the season were linearly interpolated from winter measurements (data not shown). Adding together the reconstructed hourly or weekly values of CO₂ fluxes gave seasonal estimates for gross photosynthesis, ecosystem respiration, and the NEE. Interannual differences in CO₂ fluxes were tested with Wilcoxon paired-sample test (Zar 1999). A negative sign is used to indicate CO₂ efflux from the ecosystem to the atmosphere.

Results

Effect of flooding on littoral vegetation development, photosynthesis, and respiration—According to CCA analysis, the frequently flooded communities were more similar along both transects, but the dry end communities of marsh and fen sites were characterized by forest species or species growing on nutrient-poor fen, respectively (Fig. 3). The duration of flooding had the highest interset correlation with the first axis of the ordination (0.918). The second axis correlated with sediment properties, the content of organic matter (interset correlation -0.729), and the carbon:nitrogen ratio (interset correlation 0.531) in the soil. The sediment properties separated the forest margin group of plots from the other plots on more organic (soil organic matter >50%), waterlogged soils. On the basis of CCA ordination, the fen site was divided for further analyses into upper and lower subzones, with areal covers of 72% and 28%, respectively, and the marsh site into forest margin, upper, and lower marsh subzones, with covers of 22%, 43%, and 35%, respectively.

During the wetter year, the above-ground biomass of vascular plants was significantly smaller ($Z = -4.015$, $P = 0.001$, $n = 21$)—that is, 0.3- to 0.5-fold—than during the drier year (Fig. 2). During the year with extended flooding, the stands were sparser (Fig. 4A,E) but generally taller, except for the outmost, wettest parts of the transects, where the sedges were submerged until mid-August. There, the height of the stand remained 5–20 cm lower than during the year when the water level was near the average.

The prolonged flooding delayed the seasonal maximum gross photosynthesis by up to 8 weeks, compared with that during the drier season on the same site (Fig. 4). The delay was longest in the wettest subzone (the lower marsh) and in the subzones that were seldom flooded (the forest margin and upper fen). Thus, in these zones, the reduction in the

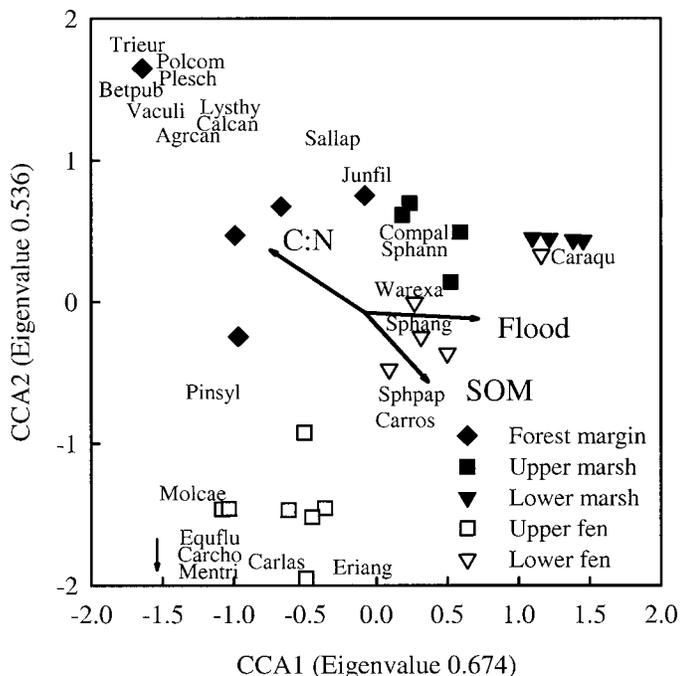


Fig. 3. CCA ordination of the Mekrijärvi vegetation communities and environmental variables: the duration of flooding in 1999 (Flood), the soil organic matter content (SOM), and the C:N ratio of the sediment. Plant species are Agrcan: *Agrostis canina* L., Betpub: *Betula pubescens* Ehrh., Calcan: *Calamagrostis canescens* (F.H. Wigg.) Roth, Caraqu: *Carex aquatilis* Wahlenb., Carcho: *Carex chorrorrhiza* L. f., Carlas: *Carex lasiocarpa* Ehrh., Carros: *Carex rostrata* Stokes, Compal: *Comarum palustre* L., Equflu: *Equisetum fluviatile* L., Eriang: *Eriophorum angustifolium* Honck, Junfil: *Juncus filiformis* L., Lysthy: *Lysimachia thyrsiflora* L., Mentri: *Menyanthes trifolia* L., Molcae: *Molinia caerulea* (L.) Moench, Pinsyl: *Pinus sylvestris* L., Plesch: *Pleurozium schreberi* (Brid.) Mitt., Polcom: *Polytrichum commune* Hedw., Sallap: *Salix lapponum* L., Sphang: *Sphagnum angustifolium* (Russow) C. Jens., Sphann: *Sphagnum annulatum* Warnst., Sphpap: *Sphagnum papillosum* Lindb., Trieur: *Trientalis europaea* L., Vaculi: *Vaccinium uliginosum* L., and Warexa: *Warnstorfia exannulata* (B.S.G.) Loeske.

observed maximum rates for gross photosynthesis was the most pronounced, being up to 88% for the forest margin. Irradiance and daily air temperature explained 24–60% of the variation in gross photosynthesis, whereas the water level explained an additional 28–55%. The only exception was the forest margin, where the period from plant emergence to the fall in the water level below the sediment surface was short (Table 1).

An increase in the respiration rate followed the lowering of the water level; in all subzones, the maximum rate was reached when the water level fell 15–20 cm below the sediment surface (Fig. 4). During the wetter season, ecosystem respiration remained at a modest level in the lower subzones, because the sediment was covered with water until September, at which time the temperature of the sediment surface had already started to decrease. The temperature at the sediment surface explained 5–47% of the variation in ecosystem respiration, and the water level explained an additional 33–71% (Table 1).

Validation of the models—The predictions of the P_g and R_{tot} models were robust to changes in variables. The change in the CO_2 flux was within $\pm 10\%$ when each variable was separately increased by 10%. When all of the variables were simultaneously increased by 10%, P_g and R_{tot} increased by 11% and 4%, respectively. The P_g and R_{tot} model estimates correlated strongly with the observed values in the independent 30% data set ($r^2 = 0.64\text{--}0.90$, $P < 0.01$, $n = 59\text{--}127$; Fig. 5). Thus, the models gave fairly accurate predictions. In the two lower subzones of the marsh site, however, the highest photosynthesis and respiration rates were both underestimated for the wetter year.

Reconstructed seasonal ecosystem CO_2 exchange—When weighted with the proportion of the subzones in the study area, both the fen and marsh sites were overall net CO_2 sources in both years. During the open-water periods in 1998 and in 1999, the fen lost 5.2 and 3.9 and the marsh lost 2.3 and 4.1 $mol\ m^{-2}$ of CO_2 , respectively (Table 2). During the season with extended flooding, seasonal photosynthesis was reduced more than respiration only in the upper fen; in four of the five zones, both the gross primary production and gaseous CO_2 losses were drastically reduced by 59–99% (for interannual differences in P_g and R_{tot} , $Z = 2.02$, $P = 0.043$, $n = 5$; Table 2, Fig. 6). In two of the subzones, the upper fen and the lower marsh, prolonged flooding decreased seasonal net ecosystem productivity and thus resulted in a 50–100% greater seasonal net loss of carbon than during near-average flooding. In contrast, the forest margin, upper marsh, and lower fen had a 60–140% greater net CO_2 loss in the drier year.

Discussion

Effect of flooding on net ecosystem productivity—Prolonged flooding did not necessarily decrease littoral net ecosystem productivity because of the contrasting effects of the depth of the water level during and after the flood, the phenology of plant emergence, and the time lags in the decomposition of organic matter. On the one hand, the seasonal net ecosystem productivity was strongly decreased when the flood water level was exceptionally high relative to the height of the vegetation stand, because high floodwater reduced photosynthesis in the air. On the other hand, net ecosystem productivity could also be drastically decreased when the lowering of the water level was sufficient to expose the surface of the sediment from water and rapidly increase ecosystem respiration. The fall in the water level after flooding depended on the sediment type (Fig. 4). As a result of the stronger water-holding capacity of fen peat compared with that of silt mud in the marsh, the groundwater level after the flood remained higher in the fen than in the marsh, even in a dry year, the aerobic layer was thinner, and the respiration lower (e.g., Billings et al. 1982). Thus, the interannual difference in postflood NEE was also smaller in the fen. Nevertheless, because both the littoral sites had organic-rich sediments—fen peat or silt mud—a low water level could result in an excess of ecosystem respiration over primary productivity, apparently partly because of enhanced decomposition of the organic matter accumulated on the site (e.g., Freeman

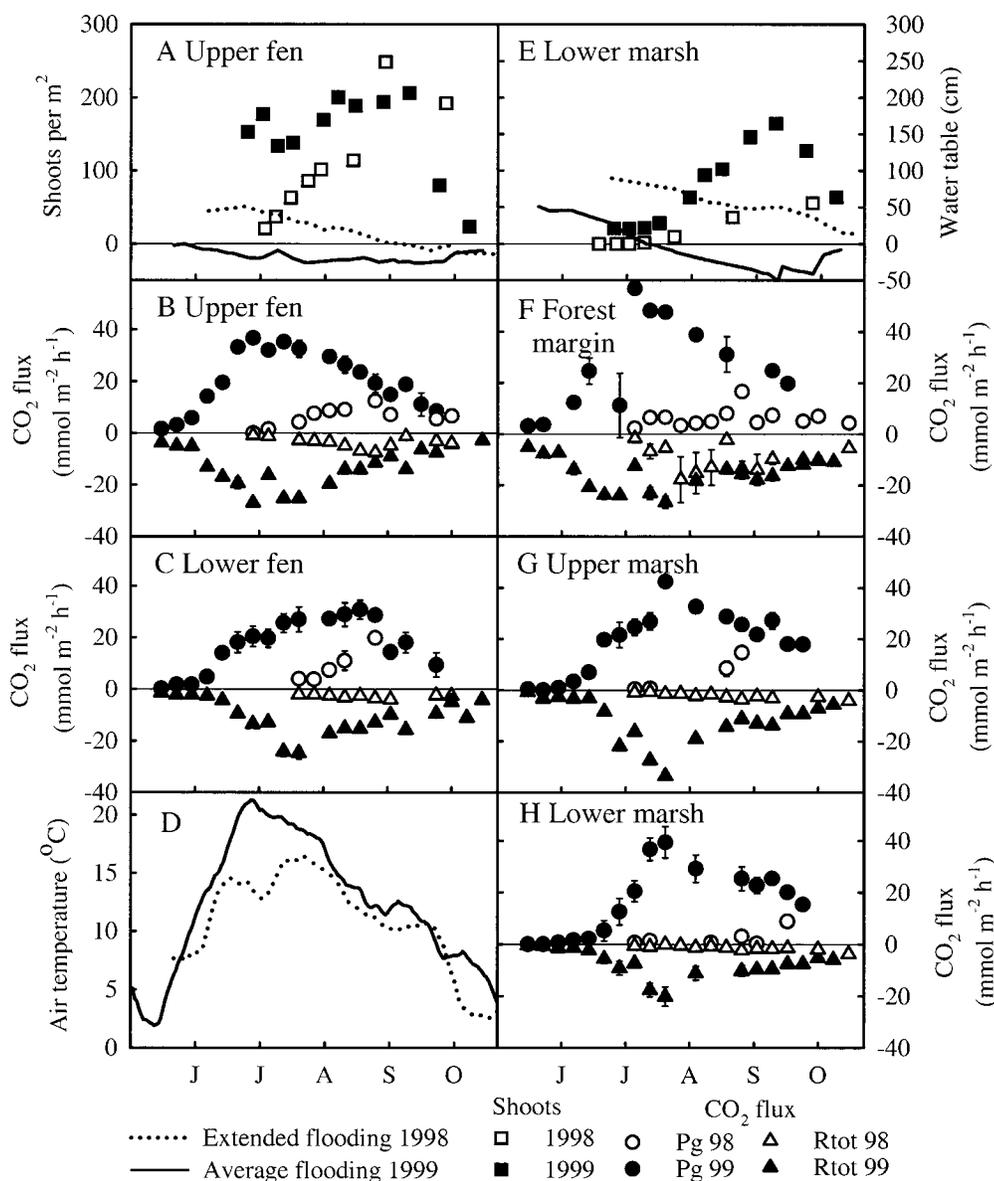


Fig. 4. Average shoot density and level of water table in the (A) upper fen and (E) lower marsh during the 1998 and 1999 study seasons. Negative values indicate water table below the sediment surface. Weekly average (\pm SE) of measured light saturated gross photosynthesis (P_g , PAR > 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and ecosystem respiration (R_{tot}) for the littoral subzones (B, C, F–H). Negative values indicate CO₂ efflux from the ecosystem. (D) The 3-week running average of mean daily air temperature during the study seasons.

et al. 2001). A similar response has been noted for mire ecosystems in dry years (Shurpali et al. 1995; Bubier et al. 2003). In contrast, in a boreal marsh on predominantly inorganic sediment, net ecosystem productivity decreased in a wet year compared with that of a dry year (deviation of the median water level ± 20 cm; Larmola et al. 2003). All of the above findings suggest that the sediment quality and the size of the soil organic matter pool, which are largely determined by long-term mean moisture conditions, could at least partly explain the contrasting response of NEE to flooding.

Furthermore, because the spring flood can flush out or-

ganic matter produced on site during preceding years or leached from the catchment, a shorter and lower spring flood could have increased the amount of organic matter remaining in the upper zones and promoted an even greater net release of CO₂ during the longer postflood period. Probably partly because of the load of organic matter from the catchment, maximum respiration rates in the littoral were higher than those of pristine fens and were close to those of cultivated organic soils in the boreal zone (Nykänen et al. 1995). In the flooded littoral, maximum respiration rates also exceeded those in littoral reed stands (Brix et al. 2001; Larmola et al. 2003). In contrast, maximum gross photosynthesis rates for

Table 1. Parameter estimates, asymptotic standard errors (ASEs) in parentheses, R^2 , and degrees of freedom for regression and residuals ($df_{\text{reg, res}}$) for the gross photosynthesis (Eq. 1) and the ecosystem respiration models (Eq. 2) for the littoral subzones at Lake Mekrijärvi.

| Parameter (ASE) | Upper fen | Lower fen | Forest margin | Upper marsh | Lower marsh |
|----------------------------------|--------------|--------------|---------------|--------------|--------------|
| Gross photosynthesis | | | | | |
| Q | 90 (27.5) | 100 (132) | 90 (18.8) | 130 (34.9) | 90 (13.4) |
| k | 430 (78.9) | 180 (72.4) | 1300 (432) | 600 (167) | 700 (164) |
| u_p | -20 (11.7) | -40 (85.2) | | -22 (7.46) | 11 (2.41) |
| t_p | -19 (4.10) | -40 (18.6) | | -17 (2.80) | -13 (2.16) |
| R^2 ($df_{\text{reg, res}}$) | 0.77 (4,293) | 0.55 (4,143) | 0.60 (2,170) | 0.79 (4,120) | 0.80 (4,143) |
| Respiration | | | | | |
| a | 4.9 (0.489) | 5.0 (0.640) | 7.6 (0.655) | 4.5 (0.520) | 2.1 (0.280) |
| b | 0.08 (0.003) | 0.09 (0.008) | 0.06 (0.005) | 0.08 (0.007) | 0.13 (0.008) |
| u_r | 0.5 (2.45) | 5 (4.09) | -4 (1.74) | 2 (1.80) | 6 (2.68) |
| t_r | -11 (1.73) | -13 (2.19) | -6 (1.37) | -5 (1.27) | -11 (1.84) |
| R^2 ($df_{\text{reg, res}}$) | 0.80 (4,283) | 0.73 (4,141) | 0.56 (4,195) | 0.82 (4,114) | 0.75 (4,143) |

Note. Q : asymptotic maximum ($\text{mmol m}^{-2} \text{h}^{-1}$), k : half-saturation constant for irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$), u_p , u_r : water table (cm) for fastest change in response of photosynthesis, respiration, t_p , t_r : direction and rate of change in water table, a : coefficient for base respiration rate, b : coefficient for dependence on temperature.

the sites were within the range of those in boreal and northern temperate sedge-dominated fens (Alm et al. 1997; Frolking et al. 1998).

Response of the plant communities to changing water level—Flooding directly reduced aerial photosynthesis, because the submergence of plants, with the associated reduction in light conditions and CO_2 supply, impedes photosynthesis and plant growth (Blom and Voeselek 1996). Cool and rainy weather, which probably also prolonged the flooding, diminished light availability for photosynthesis during midsummer, thus further reducing growth and subsequent litter production.

The plant communities responded to flooding by means of structural adaptation: fewer (Fig. 4A,E) but taller stems ensured photosynthesis in the air, as has been reported in earlier studies (Blom and Voeselek 1996). Only the stand in

the outmost littoral zones with the highest water levels remained lower. However, in the frequently flooded zones, because of its characteristic mode of growth, *C. palustre* had a high proportion of its total leaf area (photosynthetically active biomass) above the water surface even in deep water. A similar response has also been noted for *Leontodon taraxacoides* (Vill) Merat, a tolerant herb that grows on flooded grasslands (Grimoldi et al. 1999). The structural response to flooding was apparently reflected in the stand's gross photosynthesis during extended flooding, because it was higher than could be predicted on the basis of the model with only water level as a variable. This suggests that the plant species growing at such sites would be more adapted to extreme changes in the water regime than those growing in less frequently flooded sites. The proportional cover of the species growing in the lower marsh zone changed during the wetter season: *Eleocharis palustris* (L.) Roem. & Schult. and *Per-*

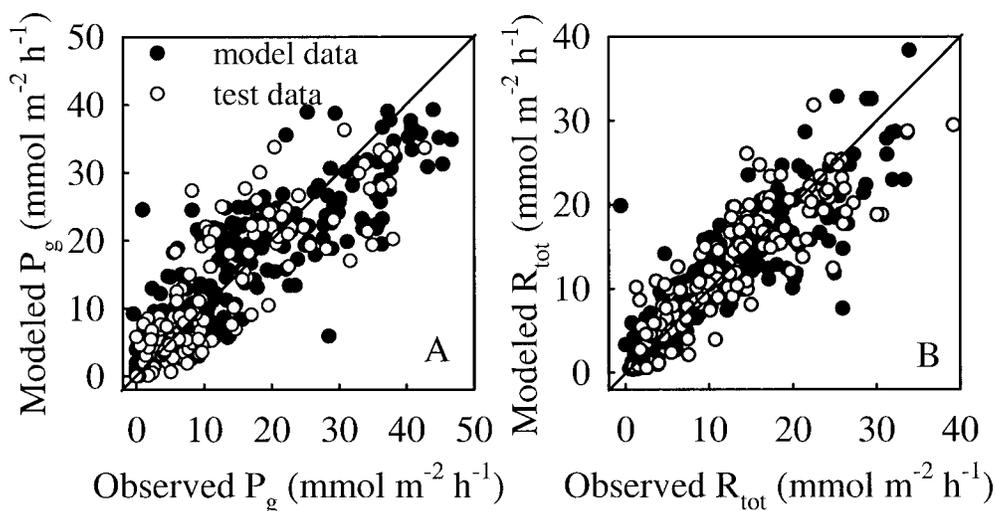


Fig. 5. Comparison of observed and modeled CO_2 fluxes for the upper fen: (A) gross photosynthesis and (B) ecosystem respiration. The data used for regression models and the independent test data are shown separately. The 1:1 line for perfect match is shown.

Table 2. Seasonal CO₂ exchange and carbon content in biomass in littoral subzones. Gross photosynthesis (P_g) and ecosystem respiration (R_{tot}) were estimated for the period of plant emergence and net ecosystem exchange (NEE) additionally for the open-water period, May–October. Negative value indicate CO₂ loss to the atmosphere. ND: not determined.

| | CO ₂ flux (mol m ⁻²) | | | | Biomass C (mol m ⁻²) | | |
|-----------------------------|---------------------------------------------|-----------|--------|----------------|----------------------------------|------|---------------------|
| | Plant emergence period | | | May–Oct NEE | Vascular shoot | Moss | Root and rhizome |
| | P_g | R_{tot} | NEE | | | | |
| 1998, extended flooding | | | | | | | |
| Upper fen | 5.00 | -11.78 | -6.78 | -7.44 | 1.3 | 13.0 | 52.3 |
| Lower fen | 4.63 | -3.52 | +1.11 | +0.72 | 1.3 | 7.7 | 28.1 |
| Fen, area weighted | | | | -5.16 | | | |
| Forest margin | 14.04 | -20.01 | -5.97 | -6.81 | 0.7 | 10.1 | 10.2 |
| Upper marsh | 0.86 | -1.58 | -0.74 | -1.44 | 1.6 | 6.1 | 70.1 |
| Lower marsh | 0.34 | -0.34 | +0.00 | -0.41 | 1.1 | 0.0 | 48.1 |
| Marsh, area weighted | | | | -2.26 | | | |
| 1999, near-average flooding | | | | | | | |
| Upper fen | 33.11 | -37.28 | -4.17 | -4.81 | 3.2 | ND | ND |
| Lower fen | 29.05 | -30.04 | -0.99 | -1.66 | 2.7 | ND | ND |
| Fen, area weighted | | | | -3.93 | | | |
| Forest margin | 33.69 | -48.67 | -14.98 | -17.68 | 2.5 | ND | ND |
| Upper marsh | 30.18 | -34.13 | -3.95 | -5.13 | 5.1 | ND | ND |
| Lower marsh | 28.71 | -21.67 | +7.04 | +5.76 | 3.0 | ND | ND |
| Marsh, area weighted | | | | -4.08 | | | |

sicaria amphibia (L.) Gray increased, whereas *C. aquatilis* became submerged (1998 vegetation data, not shown). In contrast, during the year when flooding was near average, *C. aquatilis* recovered, and its shoot density increased rapidly, probably supported by the carbohydrates stored in the large below-ground biomass (Table 2). Thus, species composition is likely to change permanently only if extreme floods are too frequent or if a permanent rise in water level is too high for the rhizomes to survive and to maintain carbohydrate reserves sufficient to sustain shoot extension through deep water in spring (Spence 1982).

During the year when the flooding pattern was near average but precipitation was low (50% of the long-term average during July–September), overall gross ecosystem photosynthesis was higher (Table 2) but apparently reduced because of drying of the moss carpet. As early as mid-July, the water contents measured for *Sphagnum papillosum* Lindb. at the fen site corresponded to 50–70% of the photosynthetic capacity at the optimal water content, and, in the forest margin, the water content indicated that there was a net release of CO₂ for *S. angustifolium* (Russow) C. Jens. (Silvola and Aaltonen 1984; Silvola 1991). In contrast, graminoid species are relatively tolerant to surface drying because they are deep-rooted and can transfer water from deeper soil layers. For example, changes in the groundwater level have no direct effect on the photosynthesis of *Eriophorum vaginatum* L. growing on peat (Tuittila et al. 1999).

Epiphytic algae can contribute up to 85% of total net annual primary production in a lake (Wetzel 1990). In the periodically inundated littoral sites, flooding is likely to promote algal growth. However, the chamber measurements include the net contribution of the photosynthetic and respiration output of algae to ecosystem-atmosphere CO₂ fluxes: early in the season, when macrophytes were submerged, both transparent and dark-chamber measurements showed a

similar net efflux from the CO₂-supersaturated lakewater to the atmosphere (Fig. 4). Nevertheless, fresh algal detritus may have enhanced the excess CO₂ release in the littoral after the flood.

Net carbon fluxes from the littoral zone—Despite the contrasting duration of the flooding period, both types of lake littoral zone showed net CO₂ efflux in both years. This is explained by the release of carbon leached from the catchment or the release of carbon accumulated on the site during previous years. For a set of Finnish forested catchments with >35% of the land area consisting of peatlands, the leaching of organic carbon ranged 0.35–0.73 mol C m⁻² yr⁻¹, half of which occurred within a period of <2 months during spring flood (Kortelainen et al. 1997). With the catchment to lake area ratio of L. Mekrijärvi, the leached organic carbon entering the lake m⁻² yr⁻¹ would be at least 10 times the area-weighted estimates of net CO₂ loss from the littoral sites during the open water period (Table 2). Lake Mekrijärvi, as is most Finnish lakes, is located on noncarbonate bedrock and overlying till, which implies a low CO₂ concentration in the groundwater. As a consequence, the organic carbon load to the lake from catchment is much higher than the inorganic carbon load. In lakewater, the average ratio of total inorganic carbon to total organic carbon was 0.22 for a set of Finnish lakes (M. Rantakari, pers. comm.).

Molot and Dillon (1996) estimated that 45–79% of the carbon from boreal forested catchment is either stored in lake sediments or degassed from lakes to the atmosphere, whereas the rest is transported downstream within the watercourse. For Finnish lakes in the size class of the sub basins of L. Mekrijärvi (1–10 km²), the average sedimentation rate would be 0.37 mol C m⁻² yr⁻¹ (Pajunen 2000). During a year with prolonged flooding, the spring flood probably flushed a higher proportion of the organic matter into deeper

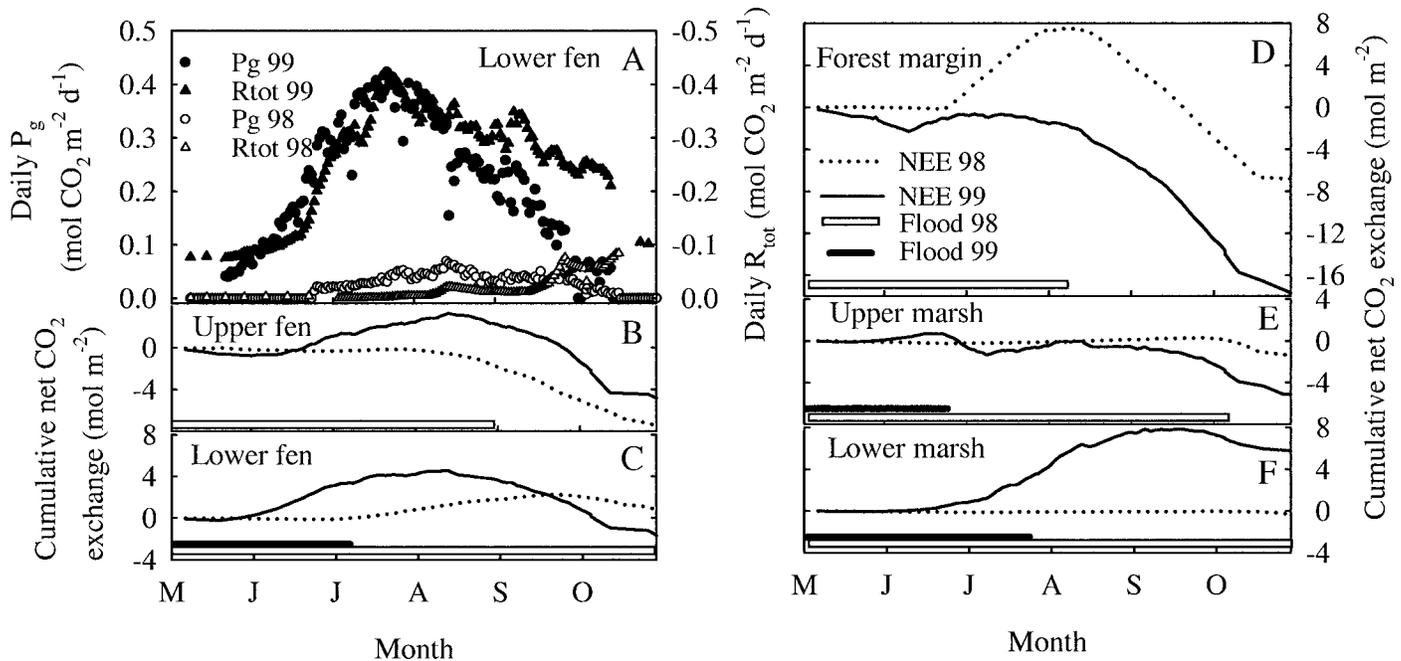


Fig. 6. An example of the seasonal patterns of gross photosynthesis and respiration (daily estimates) is shown for the (A) lower fen and (B–F) cumulative net ecosystem CO_2 exchange (NEE) and the duration of flooding are shown for all the littoral subzones at L. Mekrijärvi. Daily estimates of NEE are summed over the period of plant emergence (late June–October 1998 and May–October 1999) and weekly estimates added from early and late in the May–October periods. The increasing/decreasing slope of the curve (B–F) shows the rate of CO_2 gain/loss. The height of the curve (deviation from 0) on a specific day is the CO_2 gain/loss cumulated by that day. The duration of flooding in each subzone is indicated with horizontal lines at the bottom of each diagram (B–F).

areas of the lake, and a smaller part remained trapped in the littoral for subsequent release as CO_2 into the atmosphere. During the open-water period with near-average flooding, the net CO_2 efflux from the forest margin, the driest zone, was of the same order of magnitude as the amount of organic carbon leached per lake m^{-2} during the spring flood as based on the estimates by Kortelainen et al. (1997). This net CO_2 efflux was close to the highest efflux measured from a former peatland during the first few years after experimental flooding (18 mol m^{-2} during the open-water period; Kelly et al. 1997) or from a boreal pond (15 mol m^{-2} in 120 d during the open-water period; Roulet et al. 1997). From other littoral subzones, the estimates of net CO_2 release during the open-water season were similar to or lower than those from pelagic surface waters of the lake ($3.4\text{--}7.7 \text{ mol m}^{-2}$; T. Larmola, unpubl. data). The estimates fell within the range of those for surface waters of temperate, boreal and arctic lakes ($0.1\text{--}14.0 \text{ mol m}^{-2} \text{ yr}^{-1}$; Kling et al. 1991; Cole and Caraco 1998; Striegl and Michmerhuizen 1998; Riera et al. 1999; Casper et al. 2000; Huttunen et al. 2003).

Epilimnetic sediments are an important site of degradation of organic matter to CO_2 in lakes, as has been demonstrated even in the strong positive correlation between the concentration of pelagic surface water CO_2 and the ratio of epilimnetic sediment area to epilimnetic water volume in a set of boreal lakes (Kelly et al. 2001). In shallow humic lakes in particular, respiration in littoral sediments is therefore likely to be a major source of the littoral net CO_2 efflux, compared with potential lateral mixing of dissolved CO_2 from midlake. In addition, carbon fixed in or passed through the littoral

may contribute to the net CO_2 efflux from pelagic surface waters. In the anoxic littoral sediments, part of the carbon is converted into methane. During the open-water periods, the Mekrijärvi sites emitted methane $0.4\text{--}0.7 \text{ mol m}^{-2}$ (Juutinen et al. 2003), which is an amount of carbon that corresponds to $\sim 10\text{--}20\%$ of the net CO_2 release in moles. An extended period of flooding reduced the littoral methane losses (Juutinen et al. 2003).

Despite the potential input of allochthonous organic matter, littoral wetlands can be net consumers of atmospheric CO_2 , as has been observed in a temperate reed marsh (Brix et al. 2001) and a boreal marsh on predominantly inorganic sediment under dry conditions (Larmola et al. 2003). In wetlands, relatively small changes in production or decomposition result in large shifts in net ecosystem exchange, and the ecosystem may switch from a net CO_2 consumer to a net emitter on short timescales with small changes in the moisture conditions (e.g., Bubier et al. 2003). In the Mekrijärvi sites, a dry postflood period reduced moss photosynthesis and may have contributed to excess in respiration over production—that is, a net annual carbon loss to the atmosphere even during the year with near-average spring flooding. Similarly, a boreal mire had a net annual carbon loss because of a dry late summer even in a year with above-average precipitation (Alm et al. 1999).

The timing of spring is important for seasonal net ecosystem productivity in boreal ecosystems, because early snowmelt and warm conditions can enhance gross photosynthesis when the light levels are already high (Joiner et al. 1999). The importance of spring for seasonal net CO_2 gain

is further emphasized in the lake littoral zone. During extended flooding, the annual growth of plants is reduced, because they do not emerge from the water until late in the summer, when the level of PAR has already declined.

In the future, in the far north of Europe, the onset of the growing period may be postponed more often because of an increase in precipitation in winter (Parry 2000) and a resulting delay in the melting of the thicker snow cover in the spring. In contrast, in the transition region of the temperate and boreal zones, winter floods may become more common, but the currently high spring discharge caused by snowmelt may diminish (Vehviläinen and Huttunen 1996). Because of higher late-season temperatures, a persistent snow cover may be formed later (Parry 2000). This would further shift the snow-free period toward autumn and increase respiration late in the season. A warm, late summer, however, does not necessarily extend the growing season. Clevering et al. (2001) found that, in a warmer climate, populations of *Phragmites australis* (Cav.) Trin. Ex Steud. were not able to utilize the new, longer growing season optimally. They senesced too early, because changes in day length determined the onset of dormancy.

It is not easy to generalize the effects of flooding on littoral net ecosystem productivity. One factor that hampers this is the import of DOC from the catchment that fuels excess respiration, and another is the time lag in on-site carbon turnover. Because flooding can prevent the plants from optimally utilizing the growing season, a shorter, lower flood would extend the growing period in spring and increase the ecosystem CO₂ uptake. However, our results show that, on a seasonal scale, the littoral net ecosystem productivity does not respond consistently to changes in the flooding pattern: contrasting changes in hydrology could increase net CO₂ efflux from littoral wetlands, depending on the frequency of flooding and the littoral sediment type. The large variation in the decomposition rate on site suggests differences in the load of organic matter to the pelagic zone.

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