

Surface Peat Mass and Carbon Balance in a Hypermaritime Peatland

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ABSTRACT

Net primary production (NPP) and decomposition were measured in a suite of representative microsite types, and ^{210}Pb age was determined on near-surface peat in a hypermaritime sloping peatland in British Columbia, Canada. Hummock and depression communities had significantly higher aboveground NPP, and were characterized by higher moss NPP than other communities. Mass loss of a standard litter material was significantly different among the microcommunities, possibly because of the differences in microsite oxic conditions and water movement. Incubated litter material lost C and gained N during the 2-yr trial in all microcommunities, except for the *Sphagnum austinii* hummock, where N was lost at shallow depth. Low N content in the living *Sphagnum* and further N depletion in hummocks suggest that the hummock *Sphagnum* peat is recalcitrant to decomposition. Peat accumulation was found to be faster in hummock than in lawn communities. The hummock *Sphagnum* NPP and mass loss values were higher than published values for continental peatlands, possibly due to the wet and mild hypermaritime climate in this region. The recalcitrant nature of the litter and high NPP in hummocks likely account for rapid peat accumulation at the surface, whereas peat decomposition is most pronounced with depth, resulting in similar C sink strength as in hummocks in continental peatlands. Given that lawn community predominates, overall C sequestration capacity at the study site was estimated to be smaller than in continental peatlands. Possible range of C sink strength in sloping open peatlands in the hypermaritime region, therefore, is lower than or close to that in continental peatlands.

NORTHERN PEATLANDS are estimated to contain approximately one-third of the terrestrial C in the world because they can produce large quantities of plant biomass and sequester C as peat and organic matter after the biomass dies (Gorham, 1991). The ability of peatlands to sequester C is highly variable, depending on whether or not peat actually is formed and is able to be accumulated (e.g., Warner et al., 1993; Belyea and Warner, 1996). The C sink or source strength of peatlands is controlled by various factors such as peatland age, vegetation, and local hydrological, geochemical, and climatic conditions. Small-scale within-site features can also be highly variable to control C balance. Therefore, a more complete understanding of the C accumulation processes of individual peatlands and microsite types is critical to fully understand the potential range of C balance variation in peatlands.

The climate of the north coast of British Columbia is under strong influence of the ocean. The area receives the greatest amount of precipitation in North America, in excess of 2500 mm per year in places. Greater than

three quarters of the land surface in this region is covered by wetlands, and they are mostly peatlands (National Wetlands Working Group, 1986a; Banner et al., 1988). Although peat accumulation and C balance in oceanic peatlands have been studied well in Europe, comparatively much less is known in other parts of the northern hemisphere, especially on the Pacific north coast of British Columbia. The European study sites have been historically altered by humans. Peatlands on the north coast of British Columbia present a unique opportunity to undertake comparative studies on pristine sites. Remoteness of the north coast of British Columbia from N sources suggests that initial atmospheric N input to the system is minimal, but it is not known how such a N-deficient environment affects peat accumulation processes. The gentle to steeply sloping terrain in this hypermaritime region can also affect peat accumulation processes. For these reasons, studies on the north coast of British Columbia are more important than a mere regional study.

It is generally assumed that mild and wet hypermaritime climate stimulates plant production and decomposition, yet supporting field data are largely lacking (cf., Malmer and Wallén, 1993). Long-term peat accumulation and apparent C accumulation rates were found to be extremely low on the north coast of British Columbia (Turunen and Turunen, 2003). If we assume that peat accumulation is generally a result of slow decomposition rather than fast production (Clymo, 1984), the slow long-term peat accumulation rate is likely to be explained by relatively fast decomposition rather than low production. Malmer and Wallén (1993) calculated the mass balance of surface peat layers of *Sphagnum* hummocks in northern ombrotrophic peatlands, including the hypermaritime region of British Columbia. They found that the annual transfer of organic matter from the living moss layer to the litter peat layer is greater in hypermaritime peatlands than in continental peatlands, whereas the higher decomposition rates for hypermaritime peatlands offset the higher transfer rate. Their findings suggest that recent peat accumulation rates in hypermaritime peatlands are relatively slow because of the high decomposition rate overriding the effect of the high production. Thus, both the long-term and recent peat accumulation studies suggest that decomposition rates are much higher in hypermaritime peatlands than in continental peatlands. Unfortunately, there have been no field measurements of production and decomposition.

This study addresses mass and C balance in open peatlands on the north coast of British Columbia through a combination of field estimates of current pro-

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Abbreviations: CWHvh2, coastal western hemlock zone, very wet, hypermaritime subzone, central variant; masl, meters above sea level; NPP, net primary production.

duction and decomposition in a suite of representative microsite types and examination of the recent-past peat accumulation on near-surface cores. Three hypotheses are tested: (i) NPP, decomposition potential, and near-surface C accumulation rates are different among micro-communities in hypermaritime peatlands; (ii) NPP and decomposition potential are higher in hypermaritime peatlands than continental peatlands; and (iii) near-surface C accumulation rates are slow in hypermaritime peatlands, and this is explained by fast decomposition. The effect of global warming on the C balance in open peatlands in the region is also discussed.

MATERIALS AND METHODS

Study Site

The hypermaritime north coast of British Columbia lies in the coastal western hemlock zone, very wet, hypermaritime subzone, central variant (CWHvh2) (Klinka et al., 1991; Banner et al., 1993) in the biogeoclimatic ecosystem classification system (Pojar et al., 1987; Meidinger and Pojar, 1991). The CWHvh2 variant is situated on the Hecate Lowland, a strip of subdued, rocky terrain including the mainland coast and adjacent islands generally lower than 600 meters above sea level (masl) (Holland, 1964). The study site is a sloping open peatland in Diana Lake Provincial Park, located approximately 15 km southeast of Prince Rupert (54°13' N, 130°10' W, approximately 100 masl, Fig. 1). This site is representative of natural open peatland in the CWHvh2 variant. The bedrock is schist, gneiss, quartzite, and quartz diorite (Hutchison et al., 1979). Soils consist of Organic soils (Histosols), mostly Mesisols (Hemists) and partly Fibrisols (Fibrists) or Humisols (Saprists) (Soil Classification Working Group, 1998; Soil Survey Staff, 2003). Organic deposits (mainly *Sphagnum* and *Carex*) underlie over sandy or silty mineral and organomineral material up to 250 cm deep (Banner et al., 1993). The soil can be thin in

places with some rock outcrops. The terrain is gently sloping to the southeast, with almost flat up to 12% (Asada et al., 2003b). The open peatland is surrounded by a low productive, steeper (5–40%) wet forest composed mainly of *Tsuga heterophylla* (Raf.) Sarg., *Thuja plicata* Donn ex D. Don, *Chamaecyparis nootkatensis* (D. Don) Spach, and *Pinus contorta* Dougl. ex Loud. var. *contorta*. The open area is a mosaic of microtopographies with both bog and poor fen characteristics, being mainly five microcommunities: (i) shallow open waters dominated by *Menyanthes trifoliata* L. with frequent *Eriophorum angustifolium* Honck. (the *M. trifoliata* pool); (ii) wet depressions dominated by *Carex utriculata* Boott and *S. lindbergii* Schimp. with frequent *S. papillosum* Lindb. and *Drosera rotundifolia* L. (the *C. utriculata*–*S. lindbergii* depression); (iii) wet lawns dominated by *Rhynchospora alba* (L.) Vahl and *S. tenellum* (Brid.) Bory with frequent *Drosera anglica* Huds. and *D. rotundifolia* and locally dominant *Siphula ceratites* (Wahlenb.) Fr. (the *R. alba*–*S. tenellum* lawn); (iv) low hummocks dominated by *Racomitrium lanuginosum* (Hedw.) Brid. and *Cladina portentosa* subsp. *pacifica* (Ahti) Ahti with frequent *Kalmia microphylla* (Hook.) Heller subsp. *occidentalis* (Small) Taylor and MacBryde, *Juniperus communis* L., *Sanguisorba officinalis* L., and *Trichophorum cespitosum* (L.) Hartm. (the *R. lanuginosum* hummock), and (v) high hummocks dominated by *S. austinii* Sull. with frequent *D. rotundifolia* and *C. portentosa* subsp. *pacifica* (the *S. austinii* hummock). Some other common species in the open area are *Rhododendron groenlandicum* (Oeder) Kron and Judd, *Empetrum nigrum* L., *Andromeda polifolia* L., *Vaccinium oxycoccus* L., *Cornus canadensis* L., and *Pleurozium schreberi* (Brid.) Mitt. Scrubby *P. contorta* var. *contorta*, *C. nootkatensis*, and *J. communis* are scattered across this open area. Classification and more detailed description of each community are found in Asada (2002).

The climate of the study site is hypermaritime; cool, wet winters with little snow and warm wet summers. It is foggy and rainy year-round. The mean annual temperature in Prince Rupert is 7.0°C and the mean annual precipitation is 2500 mm. Mean monthly temperatures range from 0.8°C in January to 13.3°C in August. October is the wettest month, with 380 mm of rain. As much as 110 mm of rain falls in the driest month (July). Annual snowfall is 140 cm, although 200 mm of rain falls in the coldest month (January) (Environment Canada, 1994).

Net Primary Production

Mosses and Lichens

Nine of the most common mosses in the open peatland were selected: *S. austinii*, *S. fuscum* (Schimp.) Klingger., *S. rubellum* Wils., *S. papillosum*, *S. lindbergii*, *S. tenellum*, *S. pacificum* Flatb., *R. lanuginosum*, and *P. schreberi*. Vertical growth of *Sphagnum* spp. was measured using the cranked wire method (Clymo, 1970). As there was a risk of compaction of *Sphagnum* polsters by snow and heaving by frost in winter, the winter data were excluded from this study. Winter growth was estimated by using the relationship between the growth and climate parameters to obtain an annual growth estimate (Asada et al., 2003a). Linear growth of *R. lanuginosum* and *P. schreberi* was measured using thread markers. Thread was tied around the main stem of individual plants, and length between the point of the tie and the top of the shoot was measured to estimate the elongation. Average mass for each species was estimated from three to four core samples, with a surface area of 81 cm² cut in pure patches of each species. For *Sphagnum*, the 2.5-cm portion of the stem just below the capitulum was

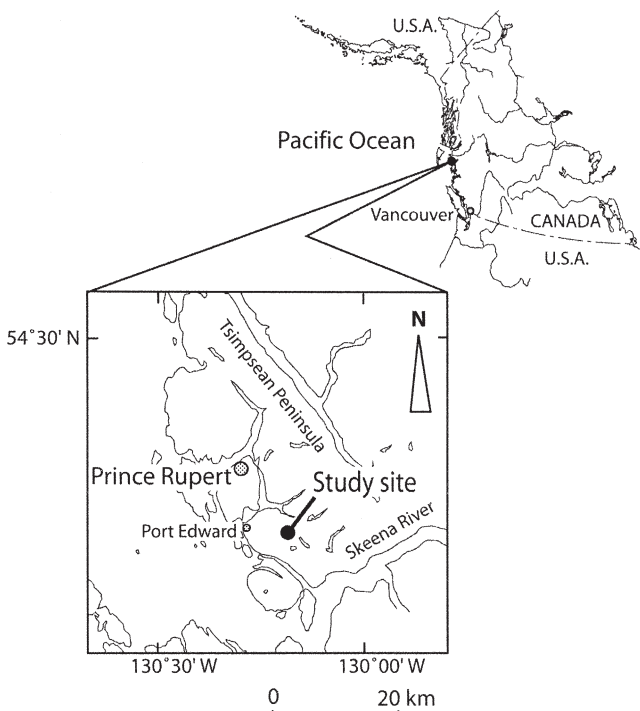


Fig. 1. Location of the study site.

collected from the core samples. For *R. lanuginosum* and *P. schreberi*, the top 2.5 cm of the main stem was collected. All samples were oven-dried at 60°C for 24 h then weighed to the nearest 0.001 g. The dry weight was converted to an average weight per centimeter per square meter for each species ($\text{g cm}^{-1} \text{m}^{-2}$). The production of each species ($\text{g m}^{-2} \text{yr}^{-1}$) was obtained by multiplying the average linear growth and the average mass per unit length per unit area. A more-detailed description of moss growth and production is in Asada et al. (2003a).

Cladina portentosa subsp. *pacifica* and *Siphula ceratites* are the major lichens in the open peatland at the study site. Aboveground biomass of *C. portentosa* subsp. *pacifica* was estimated from samples collected in late August 1999 from five 10- by 10-cm quadrats where *C. portentosa* subsp. *pacifica* covered 100% of the surface. The samples were oven-dried at 60°C for 24 h, then weighed to the nearest 0.001 g. Twenty-four podetia were randomly chosen from wet subsamples, then the length of the living portion of the podetium was measured and the number of the internodes was counted. The average annual linear growth rate was estimated by dividing the length of the living portion of the podetium by the number of the internodes, assuming that the podetium branches once a year (Scotter, 1963; Pegau, 1968; Prince, 1974; Vasander, 1981). Average annual production was estimated by dividing the biomass by the age (Prince, 1974). The biomass of *S. ceratites* was obtained in the same manner as for *C. portentosa* subsp. *pacifica*, but the age was not determined. The production of *S. ceratites* was obtained by applying the ratio of production and biomass of *C. portentosa* subsp. *pacifica* as a crude estimate.

Herbs and Shrubs

Aboveground production of herbs and shrubs was estimated by placing 50- by 50-cm quadrats in the open peatland during middle to late July in 1999, when aboveground biomass was greatest for most of the herbs at the study site. Although a small number of species had greater aboveground biomass in late spring [e.g., *Gentiana douglasiana* Bong. and *Coptis trifolia* (L.) Salisb.], their contribution to the total primary production is negligible due to their small size and minor representation at the site. All herbs and dwarf shrubs (*Andromeda polifolia*, *Cornus canadensis*, *Empetrum nigrum*, and *Vaccinium oxycoccus*) were clipped at ground level. Percentage cover and maximum height of each species were recorded in each quadrat before the clipping. The current year's leaf and stem growth was collected for other shrubs. The radial production of shrub stems was assumed to be negligible (Bartsch and Moore, 1985; Szumigalski and Bayley, 1996a). Thirty-two quadrats were sampled to include the major species in the open peatland. The sampled species encompass 98% of the total vegetation cover in the open peatland. All shrubs were sampled again in late August in 1999 (15 quadrats) when most of their growth had essentially stopped for the year. Samples were oven dried at 60°C and weighed to the nearest 0.001 g.

Belowground Net Primary Production

Belowground NPP was estimated by applying a belowground NPP/total NPP ratio available from the literature. The ratio of 0.5 was applied to *M. trifoliata* (Sjörs, 1991) and 0.88 to *C. utriculata* (Saarinen, 1996). Except for these two species, belowground NPP was estimated on a community basis. For the *M. trifoliata* pool, the *C. utriculata*-*S. lindbergii* depression and the *R. alba*-*S. tenellum* lawn communities, the ratio of 0.33 was used as the lower estimate (Weltzin et al.,

2000), and 0.70 as the higher estimate (Weltzin et al., 2000). The ratio of 0.38 was used as the lower estimate (Backéus, 1990) and 0.70 as the higher estimate (Weltzin et al., 2000) for the *R. lanuginosum* hummock and the *S. austinii* hummock communities.

Calculation of Total Net Primary Production

Total NPP from living vegetation was estimated for the five microcommunities in the open peatland. For herbs and shrubs, each species' maximum NPP value from replicate measurements was weighted by its percentage cover estimate to obtain the NPP for each species. Total community NPP was then obtained by totaling the NPP of all species in the community. Production of mosses whose cover was <1% in each community was assumed to be negligible.

The NPP for the Diana Lake open peatland as a whole was estimated by weighting the production of each community according to their relative cover in the open peatland. The percentage cover for each community was estimated from ground surveys and aerial photographs taken from a helicopter in July 1999.

Decomposition

In July 1998, *S. fuscum* was collected from the open peatland at the study site for use as a standard material in the litter bags. This species was chosen to facilitate comparisons because it is abundant at the site and has been used in many other decomposition studies (Reader and Stewart, 1972; Rosswall et al., 1975; Rochefort et al., 1990; Johnson and Damman, 1991; Szumigalski and Bayley, 1996b). The capitula of the plants were discarded, and the top 2 cm of the stems were used as the litter material. The material was air-dried and 70 to 210 mg were placed in each nylon mesh litter bag (5 by 5 cm, 0.2-mm mesh). Five litter bags were randomly chosen after being air-dried, then oven-dried (60°C, 48 h). The mean ratio of air-dried and oven-dried weight was calculated from them. To avoid possible effects that could change litter quality from the oven-drying process, the ratio obtained here was used to express the rest of the samples on an oven-dried basis without being oven-dried.

Nylon fishing line was tied to each litter bag and marked with colored beads for identification and easy retrieval. A small loop of the fishing line was knotted just next to the tie to the bag. The loop of the line was hooked on the grooved tip of a wooden stick (8 mm in diameter), and then the bags were inserted carefully to the desired depths. The bags were buried in the field on 10 and 11 Aug. 1998.

A total of 168 litter bags were incubated at three depths (10, 25, and 45 cm below the ground level) in 14 plots (1–6 plots per microcommunity) in the open peatland. Two litter bags were buried on each of the two time periods (1- and 2-yr incubation) at each depth. Additional litter bags were also incubated at a depth of 10 cm where the species in the litter bags (*S. fuscum*) dominates to make comparisons to other studies (six plots). Twelve bags were incubated for each of the two time periods.

Half of the bags at each soil depth were retrieved on 10 and 11 Aug. 1999, and the remainder was retrieved on 20 July 2000. The bags were immediately taken to the laboratory after retrieval and carefully cleaned with distilled water. Fine roots were removed from the bags with forceps. The bags were oven-dried (60°C, 48 h) and weighed to the nearest 0.001 g.

One litter bag was randomly selected from each microcommunity, depth, and incubation period treatment, respectively, for C and N analysis. The material in the litter bags was ground, and then percentage C and N were determined with a

Carlo-Erba Elemental analyzer at the Environmental Isotope Laboratory, University of Waterloo, Ontario, Canada. Amount of C and N in each litter bag was determined by multiplying the dry litter mass of each bag by the percentage values for C and N.

Depth to Groundwater Table

Polyvinyl chloride pipes with 25-mm i.d. were drilled with holes over the entire length and inserted vertically to 0.7 to 1.0 m below ground surface at all 14 plots. Depth to groundwater table was measured approximately once a week from May through August in 1998 and 1999. Three belowground zones were determined in relation to the depth to water table. In this paper, the oxic zone is defined as the area above the highest water table where it is never saturated, the anoxic zone is below the lowest water table where it is permanently saturated, and the oxic-anoxic zone is the zone of water table fluctuation where it is intermittently saturated.

Surface Peat Cores

Two short cores were collected in June 2001 by cutting surface peat columns with a metal cylinder having a surface area of 116.8 cm²: one from the *R. alba*-*S. tenellum* lawn, and the other from the *S. austinii* hummock; these are representative and contrasting microcommunities in open peatlands in the region. The cores were taken to the laboratory, and cut in half longitudinally. One-half was stored as an archive, and the other half was sliced into 1-cm-thick sections. State of decomposition was determined using the von Post humification scale (cf., Clymo, 1983). Dry bulk density was obtained by drying samples at 105°C to a constant weight. Organic matter content was estimated as loss-on-ignition after combustion at 550°C for 3 h, and total carbonate content was estimated by combustion at 950°C for 1 h multiplied by a conversion factor of 1.36 (Dean, 1974; Bengtsson and Enell, 1986).

Fifteen or 16 dried and ground samples per core were submitted to MyCore Scientific, Inc., at Deep River, Canada, for ²¹⁰Pb analysis. The concentration of ²¹⁰Pb in the samples was determined by measuring ²¹⁰Po concentration by isotope dilution α spectrometry. The constant rate of supply model was used to calculate ages of the cores (Appley and Oldfield, 1978).

Depth-dependent decomposition coefficients were estimated based on the results of ²¹⁰Pb dating, organic mass, and NPP, applying the method of Wieder (2001). The mass of organic matter beneath a unit square of peat surface between depths x and y can be expressed as

$$\begin{aligned} \text{MASS}_{x-y} = & (\text{NPP} \times \text{YR}_{x-y}) \\ & \times \exp[-(k_{0-a} \times \text{YR}_{0-a} \\ & + k_{a-b} \times \text{YR}_{a-b} + \dots \\ & + k_{x-y} \times \text{YR}_{x-y})] \end{aligned} \quad [1]$$

where MASS_{x-y} is the ash-free mass of organic matter at a depth of $x-y$ cm of peat section per unit square, NPP is the annual net primary production per unit square at the peat surface, YR_{x-y} is the number of years represented by the $x-y$ cm section, k_{x-y} is the exponential decomposition coefficient for the $x-y$ cm section (per year). Thus, a peat core sectioned and dated into z slices possesses z simultaneous equations with z unknowns, which are the exponential decomposition k values, as MASS_{x-y} and NPP are measured in this study. The solutions for the k values are:

$$k_{0-a} = (\text{YR}_{0-a})^{-1} \times \ln[\text{NPP} \times \text{YR}_{0-a} \times (\text{MASS}_{0-a})^{-1}] \quad [2]$$

for the uppermost section and

$$k_{x-y} = (\text{YR}_{x-y})^{-1} \times \ln[(\text{MASS}_{w-x} \times \text{YR}_{x-y}) \times (\text{MASS}_{x-y} \times \text{YR}_{w-x})^{-1}] \quad [3]$$

for the sections beneath the top section. Mean annual mass loss from the $x-y$ cm section was estimated by multiplying MASS_{x-y} by k_{x-y} divided by YR_{x-y} . Mean C concentration of 49.3% based on the measurements of peat cores from the same site (Turunen and Turunen, 2003) was used to estimate the C balance.

Statistical Analyses

Estimates of aboveground, belowground, and total NPP among microcommunities were compared using ANOVAs. The normality of the data distribution was evaluated by Kolmogorov-Smirnov one-sample test and the homogeneity of variance by Levene's test. Log-transformation was effective to improve the normality for some NPP data. Outliers in the mass loss data were recognized using box plots and excluded from further statistical analyses. As the normality of the distribution and the homogeneity of variance were assumed, the remaining mass loss data were not transformed. Two-way ANOVA was used to analyze the differences in mass loss among microcommunities and incubation depths for each incubation period. The mass loss data in the *S. austinii* hummock were further analyzed with one-way ANOVA with oxic condition as a fixed factor because the *S. austinii* hummock was the only microcommunity with complete well-developed zones (oxic, oxic-anoxic, and anoxic). Type III sum of squares was used for all ANOVAs because sample sizes were unequal (Quinn and Keough, 2002). Post hoc testing was performed with Tukey's HSD (honestly significant difference) for the data set whose homogeneity of variance was assumed and Dunnett T3 was used when it was not assumed. All statistical analyses were performed with SPSS Version 10.0.5 (SPSS, 1999).

RESULTS

Net Primary Production

Aboveground total NPP was different among the microcommunities (Table 1). The *S. austinii* hummock had the highest aboveground NPP, and then the *C. utriculata*-*S. lindbergii* depression. These two microcommunities and the *R. lanuginosum* hummock had significantly higher aboveground NPP than all others. Mosses were the greatest contributor to the aboveground total NPP for all of the microcommunities except for the *M. trifoliata* pool. Any microcommunity having high moss NPP had high aboveground total NPP, and vice versa. Contribution of shrubs to the aboveground total NPP was only 7 to 10% in the two hummock microcommunities, and even smaller in the others. Total aboveground NPP correlated to depth to groundwater table. The greater the mean depth, the higher the total aboveground NPP (Fig. 2). Shrubs showed this relationship clearly, but it was not the case for herbs and lichens.

Total (above- and belowground) NPP was highest in the *S. austinii* hummock and the *C. utriculata*-*S. lindbergii* depression. Differences among microcommunities

Table 1. Estimated net primary production (NPP) for the five representative microcommunities at the Diana Lake study site. Values are means \pm SE. Significant differences between means are indicated by different letters for each component of NPP (Tukey's HSD or Dunnett T3, $P < 0.05$). Belowground NPP with possible range were estimated using belowground NPP/total NPP ratios available from previous studies. See text for more detailed explanation about the estimation methods.

Microcommunity	Aboveground	Belowground		Total		n
		Lower	Higher	Lower	Higher	
		$\text{g m}^{-2} \text{yr}^{-1}$				
<i>Menyanthes trifoliata</i> pool	104.7 \pm 23.5b	85.5 \pm 18.6a	164.6 \pm 40.0ab	190.2 \pm 41.5bc	269.3 \pm 62.8bc	5
<i>Carex utriculata</i> - <i>Sphagnum lindbergii</i> depression	300.9 \pm 32.4a	121.5 \pm 38.8a	194.6 \pm 41.5ab	422.5 \pm 63.8ab	495.6 \pm 51.8a	9
<i>Rhynchospora alba</i> - <i>Sphagnum tenellum</i> lawn	163.6 \pm 23.6b	15.1 \pm 2.9b	71.6 \pm 13.9b	178.7 \pm 25.2c	235.2 \pm 32.9c	14
<i>Racomitrium lanuginosum</i> hummock	291.3 \pm 30.5a	43.9 \pm 5.0a	164.7 \pm 19.2a	335.2 \pm 30.4ab	456.1 \pm 35.4ab	9
<i>Sphagnum austinii</i> hummock	402.4 \pm 14.5a	24.1 \pm 9.1ab	91.8 \pm 34.6ab	426.5 \pm 23.5a	494.2 \pm 48.9ab	5
One-way ANOVA P value	<0.001	<0.001	0.007	<0.001	<0.001	

were smaller for total NPP than for aboveground NPP (Table 1). This is because moss contribution to the aboveground NPP is greater than vascular plant contribution in the *S. austinii* hummock, whose aboveground total NPP is the highest. The reverse is true for the *M. trifoliata* pool, whose aboveground total NPP is the lowest. Given that belowground production is supplied mainly by vascular plants, the *M. trifoliata* pool has high belowground production, and the *S. austinii* hummock has the least.

Approximately 90% of the surface of the study site is covered by the five microcommunities studied. The *R. alba*-*S. tenellum* lawn covered about 75% of the area. The *R. lanuginosum* hummock occupied 10%, and the other communities occupied 3% in total. Total NPP in the open peatland as a whole was estimated by weighting the NPP of each microcommunity according to its percentage cover. Overall aboveground NPP was estimated at $175 \text{ g m}^{-2} \text{yr}^{-1}$, and total NPP at 195 to $257 \text{ g m}^{-2} \text{yr}^{-1}$.

Decomposition

Mean mass loss (percentage of the initial mass) of the standard litter material for each microcommunity ranged from 13.5 to 19.3% after 1-yr incubation (mean loss = 15.9%) (Table 2). A minor amount was lost in the second year. Mass loss was significantly different among the microcommunities. The greatest loss of mass occurred in the *S. austinii* hummock, and the smallest in the *M. trifoliata* pool for both incubation years. The *S. austinii* hummock is the only microcommunity that has a well-developed oxic zone, and the *M. trifoliata* pool is always waterlogged (Table 3). Mass loss decreased with depth, and the difference between 10 and 45 cm was significant for both of the incubation periods (Table 2). The differences in mass loss among the three oxic conditions were further tested in the *S. austinii* hummock because each incubation depth (10, 25, or 45 cm) is situated within each oxic condition (oxic, oxic-anoxic, or anoxic) respectively in this community (Table 4). Mass loss was significantly greater in the oxic zone than in the oxic-anoxic and in the anoxic zones. Mean mass loss was the least in the deepest anoxic zone, but the difference from that in the oxic-anoxic zone was not significant.

Carbon was lost from the litter through time, and the

loss was greater in the first year than in the second year (Fig. 3). Nitrogen generally increased through time, and the change was more variable than C. In most cases, small gain or loss was observed in the first year and greater gain was observed in the second year. An exceptional trend of N loss was observed at the 10-cm depth in the *S. austinii* hummock.

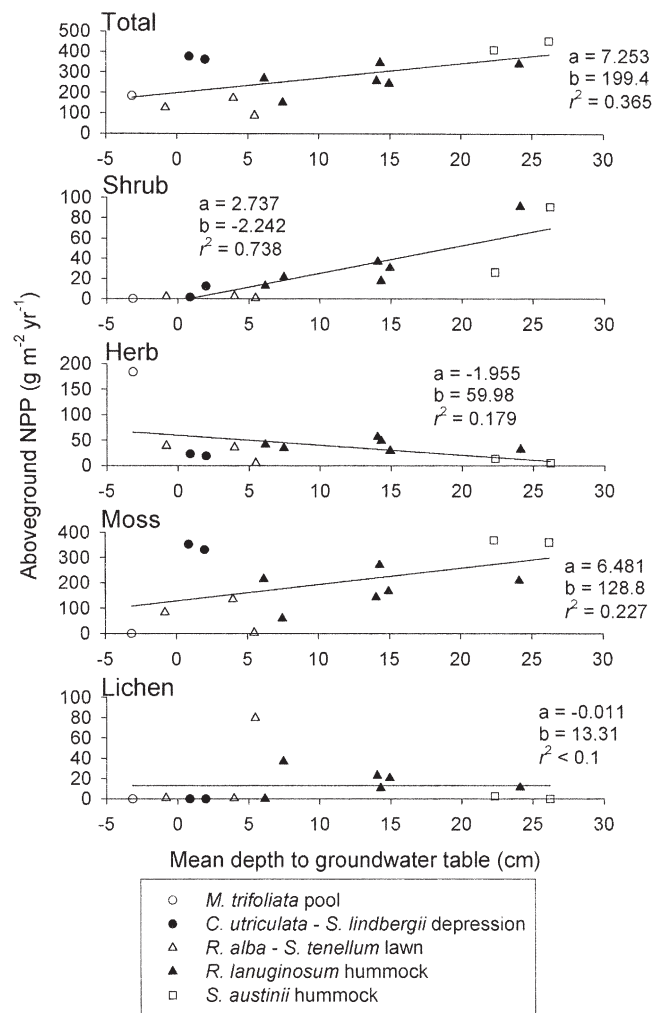


Fig. 2. Aboveground net primary production (NPP) in relation to mean depth to groundwater table at the Diana Lake study site. Two constants and r^2 values are for the linear regression $y = ax + b$. Note that the vertical scales are not consistent.

Table 2. Percentage weight mass losses of a standard litter (*Sphagnum fuscum*). Values are means \pm SE. A two-way ANOVA was performed for each incubated period separately with microcommunity and depth as the main effects. Significant differences are indicated by different letters for each incubated period within a main effect (Tukey's HSD, $P < 0.05$).

	1 year		2 years	
	Mass loss	<i>n</i>	Mass loss	<i>n</i>
Microcommunity	%		%	
<i>Menyanthes trifoliata</i> pool	13.5 \pm 1.3c	6	13.7 \pm 1.3b	6
<i>Carex utriculata</i> – <i>Sphagnum lindbergii</i> depression	19.0 \pm 0.9a	12	23.3 \pm 0.9a	12
<i>Rhynchospora alba</i> – <i>Sphagnum tenellum</i> lawn	15.7 \pm 0.8bc	18	17.3 \pm 0.8b	17
<i>Racomitrium lanuginosum</i> hummock	14.5 \pm 0.6c	36	17.5 \pm 0.5b	35
<i>Sphagnum austinii</i> hummock	19.3 \pm 1.0ab	11	22.5 \pm 1.0a	11
Depth, cm				
10	17.9 \pm 0.8a	27	21.3 \pm 0.7a	26
25	16.7 \pm 0.7ab	28	17.7 \pm 0.7b	28
45	14.5 \pm 0.7b	28	17.7 \pm 0.7b	27
Two-way ANOVA <i>P</i> value				
Microcommunity	<0.001		<0.001	
Depth	0.004		<0.001	
Microcommunity \times depth	0.165		0.319	

Surface Peat

The *S. austinii* hummock core was poorly decomposed *Sphagnum* peat dominated by remains of *S. austinii*, underlain by moderately decomposed *Sphagnum/Carex* peat (Fig. 4). The *R. alba*–*S. tenellum* lawn core was mostly moderately to well decomposed *Sphagnum/Carex* peat throughout the core except a thin layer at the surface. The increases in dry bulk density and humification with depth roughly synchronize for each of the cores respectively. The increase in values occurs in the zone of groundwater table fluctuation.

Age increase with depth is much steeper in the *R. alba*–*S. tenellum* lawn core than in the *S. austinii* hummock core (Fig. 5). The depth for 200 years old before 2001 occurs at approximately 18 cm in the *R. alba*–*S. tenellum* lawn core and at 38 cm in the *S. austinii* hummock core. Both cores show decreasing intervals of between years with depth, resulting in concave curves, which is more pronounced for the *S. austinii* hummock core.

Relationships between cumulative mass loss and depth fit well with exponentially rise-suppressed curves for both of the cores (Fig. 6). These empirically obtained curves were used to estimate the C balance in near-surface peat. The results show both microcommunities are a sink of C, and the C sequestration capacity is greater in the *S. austinii* hummock (Table 5). In the *R. alba*–*S. tenellum* lawn, however, the C balance could be close to equilibrium in thicker surface peat. This is suggested by the low estimation value obtained by extending the theoretical cumulative mass loss curve only deeper to 40 cm (Table 5).

DISCUSSION

Mass and Carbon Balance in Hummock Community

This study indicates that NPP in hummock communities is high in hypermaritime peatlands. Comparison of NPP values from *S. fuscum* hummocks, a primary component in northern peatlands, shows that the NPP is higher in this hypermaritime peatland than in continental peatlands (Fig. 7). Such high production must be largely due to the climate in the region. Positive correlations of *Sphagnum* growth with precipitation and low temperature thresholds for their growth have been shown at the study site (Asada et al., 2003a). It suggests that the abundant precipitation in the region is advantageous for *Sphagnum* growth, and the mild temperature throughout the year makes even winter growth possible. Hence, *Sphagnum* is able to grow almost year-round under oceanic mild climate as opposed to 8 mo or less in continental sites.

The potential for decomposition is also higher in the hypermaritime peatland than in other continental peatlands. Despite our more conservative approach to derive estimates by using fine mesh litter bags, plants without capitula, and fresh samples, mass loss values were still greater than those from other geographic locations (Table 6; Johnson and Damman, 1993). Some possible reasons for such high decomposition rates are: (i) mild temperatures throughout the year under oceanic influence allow decomposers to be active year round; and (ii) a steady supply of precipitation and the sloping terrain maintain active water movement that provides

Table 3. Oxidic conditions of the litter-incubated depths and mean depth to groundwater table for the five representative microcommunities at the Diana Lake study site. The negative number for the groundwater table means aboveground. See text for the definitions of the three oxidic conditions.

	<i>Menyanthes trifoliata</i> pool	<i>Carex utriculata</i> – <i>Sphagnum lindbergii</i> depression	<i>Rhynchospora alba</i> – <i>Sphagnum tenellum</i> lawn	<i>Racomitrium lanuginosum</i> hummock	<i>Sphagnum austinii</i> hummock
Depth, cm					
10	anoxic	anoxic	oxic–anoxic	oxic–anoxic	oxic
25	anoxic	anoxic	oxic–anoxic	oxic–anoxic	oxic–anoxic
45	anoxic	anoxic	anoxic	oxic–anoxic	anoxic
Groundwater table, cm	–3.1	1.4	2.9	13.5	24.3

Table 4. Percentage weight mass losses of a standard litter (*Sphagnum fuscum*) in the three oxic conditions in the *Sphagnum austinii* hummock community. A one-way ANOVA was performed for each incubated period separately. Values are means \pm SE. Significant differences between means are indicated by different letters for each incubated period (Tukey's HSD, $P < 0.05$).

Oxic condition	1 year		2 years	
	Mass loss	<i>n</i>	Mass loss	<i>n</i>
	%		%	
Oxic	23.7 \pm 1.2a	3	27.4 \pm 1.2a	3
Oxic-anoxic	17.7 \pm 1.0b	4	20.6 \pm 1.0b	4
Anoxic	16.5 \pm 1.0b	4	19.5 \pm 1.0b	4
One-way ANOVA <i>P</i> value	0.003		0.002	

decomposers with a constant supply of oxygen and nutrients and contributes to comminution and erosion of small particles from peat layers.

The ability for hummock litter to decompose could be lower in this hypermaritime region than in continental regions. Nitrogen content in litter is known to affect its ability to decompose (e.g., Malmer and Holm, 1984). Percentage N in fresh *S. fuscum* litter was low at our study site ($\bar{x} = 0.247\%$, SE = 0.0014, $n = 4$) compared with data from other regions (Malmer and Holm, 1984; Szumigalski and Bayley, 1996b). Such low N values could be due to the remoteness of the study site from human sources of atmospheric N such as from industry, agriculture, and urban areas (Malmer and Holm, 1984; Vardy et al., 2000). Nitrogen is further depleted in the oxic zones of hummocks after incubation. Net N loss occurred at the 10-cm depth (oxic zone) in the *S. austinii* hummock community, whereas other microcommunities and deeper depths in the *S. austinii* hummock community showed net gains (Fig. 3). The N loss could be related to leaching, consumption by microorganisms, uptake by plants, and denitrification (Berg and Staaf, 1981; Swift et al., 1979) whereas gain could be related to N entering the litter bags from the N-richer surroundings. This increasing N richness with depth is created by the preferential C loss during peat decomposition (Malmer and Holm, 1984; Kuhry and Vitt, 1996). The increase in N content with depth in surface peat can be greater than twofold in ombrotrophic peatlands (cf., Malmer and Holm, 1984). Nitrogen immobilization would then follow through assimilation by microorganisms in the litter bags. Scheffer et al. (2001) showed that most of the actual N loss in the early stages of *Sphagnum* litter decomposition was attributed to leaching. Leaching causes the net N increase to be smaller for the first year than the second year even if the N immobilization activity were the same during both years (cf., Berg and Staaf, 1981; Staaf and Berg, 1982). This net N loss-gain contrast shown between the *S. austinii* hummock and the other less *Sphagnum*-dominated communities at our site agrees with the observation shown at much greater landscape scale such as between *Sphagnum*-dominated and *Carex*-dominated peatlands in the central Netherlands (Scheffer et al., 2001). The N depletion from the hummock *Sphagnum* would further enhance its intrinsically recalcitrant nature explained by recalcitrant com-

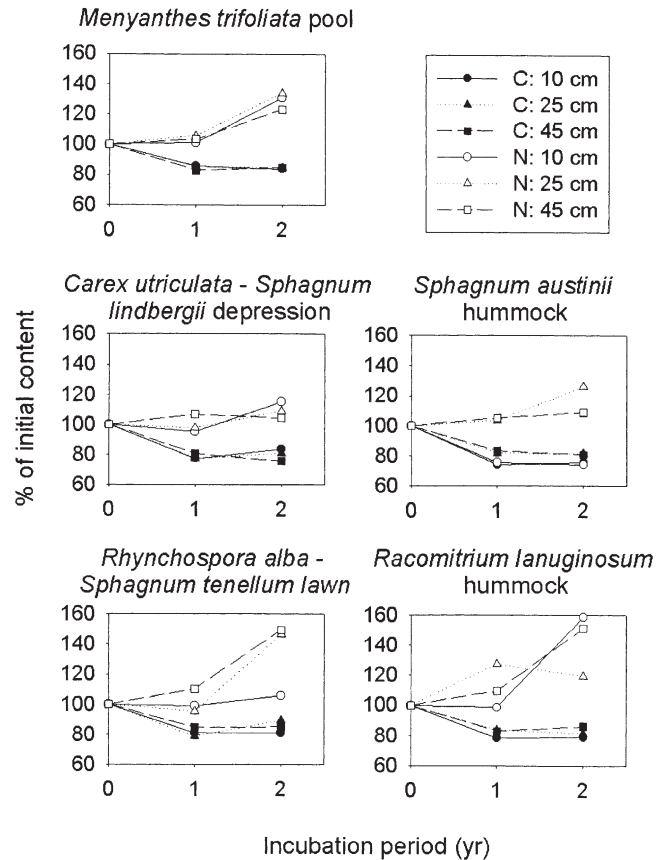


Fig. 3. Carbon and N loss and gain of a standard litter (*Sphagnum fuscum*) incubated at the three depths at the Diana Lake study site.

pounds such as lignocellulose (Benner et al., 1984) and decay inhibition by organic metabolites in *Sphagnum* cells such as phenolics and uronic acids (Rudolph and Samland, 1985; Verhoeven and Toth, 1995; Verhoeven and Liefveld, 1997). This small decomposability and high NPP would explain the thick less-humified layer above the zone of water table fluctuation (Fig. 4), and greater C gain in the oxic zone (Table 5).

The decomposition potential of the hypermaritime environment overpowers the recalcitrant litter quality of hummock *Sphagnum* during a longer term. Despite the higher NPP and the greater mass remaining in the initial stage of peat accumulation (Fig. 7), net C gain in the top 40 cm of peat (Table 5) is about the same or even lower than that for continental peatlands ($34\text{--}52\text{ g C m}^{-2}\text{ yr}^{-1}$; Wieder, 2001). This illustrates the magnitude of decomposition potential of peat in hypermaritime environments.

Malmer and Wallén (1993) have suggested from their stratigraphical study of near-surface cores that *Sphagnum*-dominated hummocks have higher NPP in hypermaritime peatlands than in less-oceanic peatlands, whereas the higher decomposition rate in hypermaritime peatlands offsets the higher peat accumulation rate. Our field estimates of NPP and decomposition in this study support their assumptions and underscore the ecological importance of hypermaritime climate on peatlands.

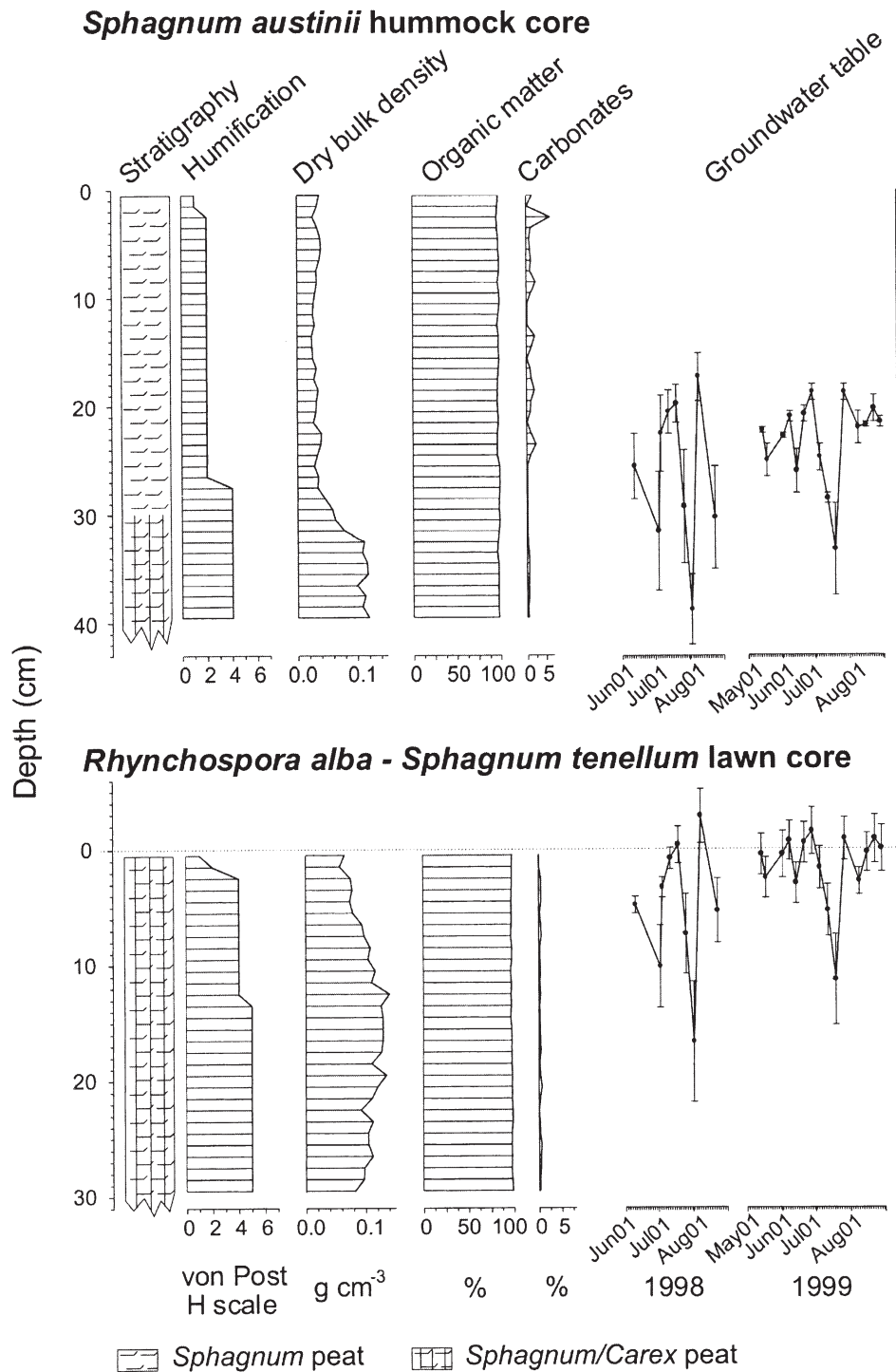


Fig. 4. Stratigraphy, humification, loss-on-ignition, and groundwater table (Mean ± SE) diagrams for the short cores at the Diana Lake study site. Symbols for stratigraphy represent the major components of the peat.

Mass and Carbon Balance in Lawn Community

The NPP for the *R. alba*-*S. tenellum* lawn was lower than for the hummock communities (Table 1). This community consists predominantly of mosses and herbs with low production, and contains few shrubs due to the high water table (Fig. 2). Effect of the hypermaritime climate and the sloping topography on decomposition potential

is expected to be as great as in hummocks. Litter decomposability of lawn species is known to be greater than that for hummock species (Johnson and Damman, 1991; Belyea, 1996), and N content in litter increases with time in lawns although its initial content in fresh litter could be low (Fig. 3).

Although the peat layers of *R. alba*-*S. tenellum* lawn do not have oxyc zone which has higher decomposition

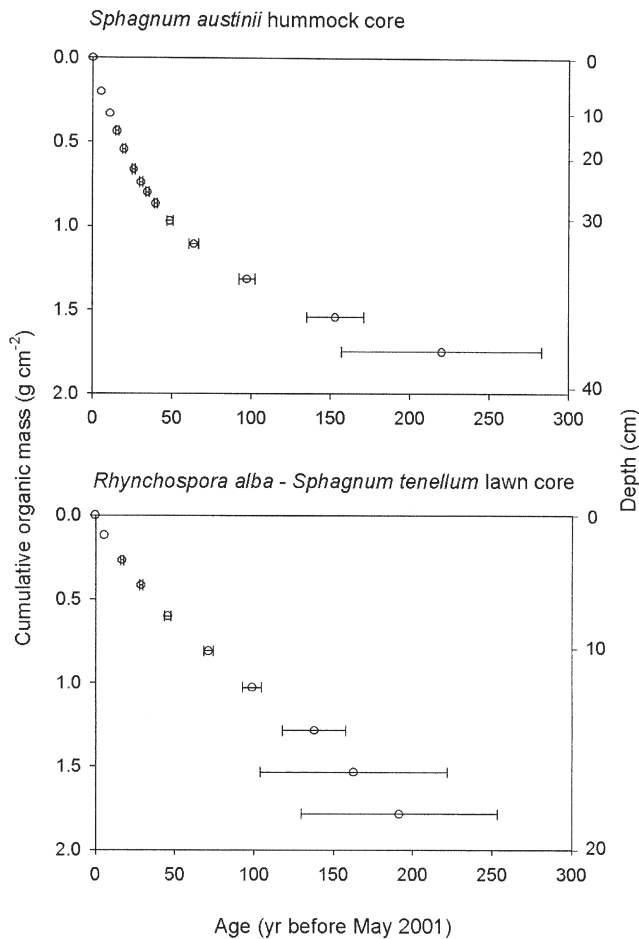


Fig. 5. Peat age in relation to depth for the short cores at the Diana Lake study site. Ages were dated by ^{210}Pb . Depth is expressed as cumulative (ash-free) dry mass (left-hand axis) and as length (right-hand axis). Ages are expressed as years before 2001. Means \pm SD are shown.

potential than the other zones, net C gain was small in the near-surface peat in this microcommunity (Table 5). This would be explained by low NPP in this microcommunity, high decomposition potential of the region, and relatively greater litter decomposability of lawn litter than hummock litter.

Mass and Carbon Balance in Hypermaritime Open Peatlands

The NPP and decomposition rate are greatly variable among the microcommunities, thereby leading to differences in peat accumulation rate and C balance in the regional open peatlands. The result showed that the study site had relatively low NPP compared with other *Sphagnum*-dominated open peatlands (Table 7). This low NPP is explained by the dominance of the *R. alba*-*S. tenellum* lawn. Overall C sequestration capacity of the study site can be estimated to be small because the capacity of this lawn community is small (Table 5).

There are many kinds of open peatlands in the region (MacKenzie and Moran, 2004), and some are dominated

by *S. austinii* hummocks. Greatest C may be sequestered in such peatlands. However, the results from the Diana Lake site suggest that even peatlands dominated by *S. austinii* hummocks may not exceed continental peatlands in terms of C sink strength, owing to high decomposition potential in hypermaritime sloping peatlands. Nevertheless, we cannot conclude yet that small C sequestration capacity is the general feature associated with hypermaritime peatlands. Some peatlands dominated by *S. austinii* seem to occur on relatively flat lowlands in the region, such as on Graham Island. Such areas are perhaps hydrologically less active than sloping systems, thus decomposition potential can be expected to be lower. The great mass loss in the *C. utriculata*-*S. lindbergii* depression, despite its constant waterlogged conditions (Table 3), might be explained by the distribution of this community in hydrologically active peat channels where water flow is continuous, which might be conducive to physical or chemical degradation of litter. This might suggest that decomposition potential is probably much higher in sloping systems than those on flat terrain. Lowland peatlands dominated by *S. austinii* likely have greater C sequestration capacity than sloping peatlands due to their higher NPP and relatively less decomposition.

Effect of Global Warming

Hypermaritime peatland ecosystems might be expected to be sensitive to climate change. According to global climate change prediction models, the north coast of British Columbia is expected to experience temperature rise greater than the global average, and precipitation is expected to increase 5 to 20% in winter. Atmospheric CO_2 is predicted to increase 48 to 166% by the year 2100 (IPCC, 2001). Under this scenario, NPP would be either enhanced or retarded in peatlands on the north coast. Shrub NPP likely will increase. Higher temperature in summers would cause lowered groundwater tables, and it would reduce detrimental anoxic conditions for shrubs (cf., Fig. 2; Szumigalski and Bayley, 1997). Higher temperature and higher atmospheric CO_2 concentration would enhance their photosynthesis. How herb NPP might change is difficult to predict, but greater species turnover would occur as sites changes from hydric to much drier types. Prediction of how moss NPP might change is also difficult. While moderately higher temperature than current conditions would seem advantageous for their growth, drier summers may have negative effects (Asada et al., 2003a). Milder and wetter conditions in winter would enhance their growth (Asada et al., 2003a). The results from elevated CO_2 concentration experiments on the growth of *Sphagnum* are not consistent, although most of them showed enhanced growth (Silvola, 1985, 1990; Jauhiainen and Silvola, 1996; Jauhiainen et al., 1996), and so similarly might occur on the north coast.

Global warming most likely would cause a shift along the depression/pool-lawn-hummock gradient toward drier communities as groundwater table decreases because of the rise in temperature and trend toward drier

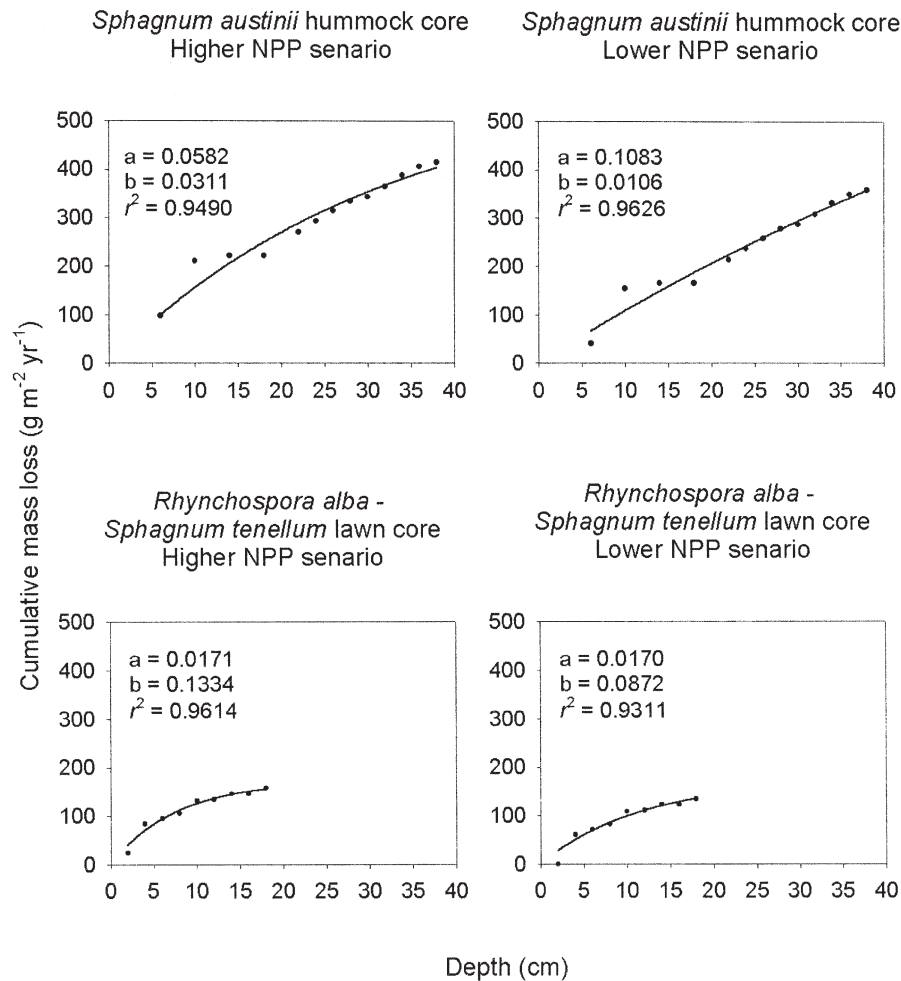


Fig. 6. Cumulative mass loss with depth for the short cores at the Diana Lake study site. Depth-dependent decomposition rates were estimated based on the results of ²¹⁰Pb dating, organic mass, and net primary production (NPP). See text for details. Two constants and r^2 values are for the regression curve $y = a \times [1 - \exp(-b \times x)]$. Both the lower and higher NPP scenarios were used for the *Sphagnum austinii* hummock core and the *Racomitrium lanuginosum*-*S. tenellum* lawn core.

summers. Existing hummock *Sphagnum* species, however, might persist in open peatlands because they possess an ability to withstand dry conditions, owing to their compact growing form that helps to preserve moisture (Rydin, 1985; Aravena and Warner, 1992). Prevalence of hummock *Sphagnum*-dominated peatlands in conti-

mental regions where summers are hotter and drier than in north coast of British Columbia would support this prediction (National Wetlands Working Group, 1986b). *Racomitrium lanuginosum* might also increase dominance in open peatlands because of its capacity to withstand drought (Tallis, 1959). Alternatively, global warming

Table 5. Estimated C balance in surface peat in the two microcommunities at the Diana Lake study site. Cumulative mass loss with depth was estimated using regression equations in Fig. 6. Carbon balance was estimated as a range using the lower and higher estimation values of total net primary production (NPP) in Table 1.

Depth	C gain			
	<i>Sphagnum austinii</i> hummock		<i>Rhynchospora alba</i> - <i>Sphagnum tenellum</i> lawn	
	Lower NPP	Higher NPP	Lower NPP	Higher NPP
	g m ⁻² yr ⁻¹			
0-HWT [†]	120.8	124.2	-	-
0-LWT [‡]	30.2	42.6	23.8	40.7
0-dated depth by ²¹⁰ Pb [§]	33.2	44.7	21.7	39.3
0-40.0 cm	25.8	39.4	6.9	32.1

[†] Mean depth to highest groundwater table (HWT); 17.3 cm for *S. austinii* hummock and negative (aboveground) for *R. alba*-*S. tenellum* lawn.

[‡] Mean depth to lowest groundwater table (LWT); 38.8 cm for *S. austinii* hummock and 16.7 cm for *R. alba*-*S. tenellum* lawn.

[§] 38.0 cm (≈220 yr of accumulation) for *S. austinii* hummock and 18.0 cm (≈192 yr of accumulation) for *R. alba*-*S. tenellum* lawn.

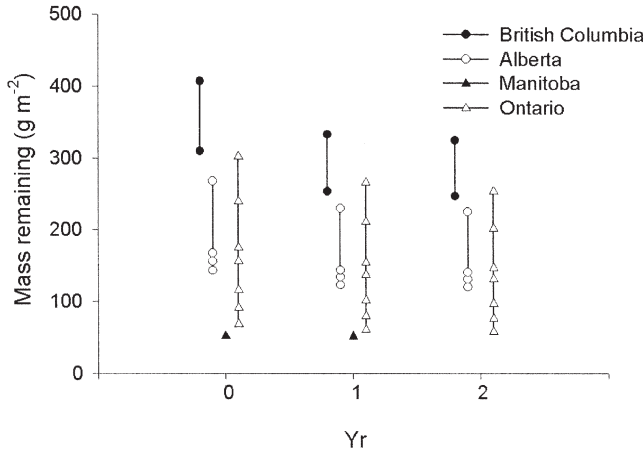


Fig. 7. Change in mass of *Sphagnum fuscum* litter in litter bag after one and two years of decomposition at four sites in Canada. Litter bags were incubated in the original habitat of *S. fuscum*. The mass remaining at Year 0 means initial annual production of *S. fuscum*. British Columbia (54°13' N, 130°10' W), this study; Alberta (54°41' N, 113°28' W), Szumigalski and Bayley (1997) and Thormann and Bayley (1997b); Manitoba (49°53' N, 95°54' W), Reader and Stewart (1971, 1972); Ontario (49°40' N, 93°43' W): Rochefort et al. (1990). Highest value of the initial annual production in British Columbia includes the estimate of winter growth, and the lowest value shows the production from May to November. Initial annual NPP in Manitoba includes weight of capitula (Reader and Stewart, 1971).

may shift hummock communities to different communities altogether. Hummocks often serve as dry islands for trees to invade, and increased dryness by global warming would encourage more trees to establish. Once trees have established on hummocks and reached some size, they contribute to the extermination of *Sphagnum* and the site modifications that are favorable for tree growth (Ohlson et al., 2001). Vegetation change from open to more forested landscape may happen accordingly, starting from the loci previously dominated by hummock communities. This momentum toward vegetation change may reverse the paludification that is currently the case at the study site (Turunen and Turunen, 2003).

Decomposition of peat will be enhanced because a thickened oxic zone (Table 4) and a rise in soil temperature would be beneficial for aerobic decomposers (Swift et al., 1979). Hence, peat accumulation rate will decrease if the change in total NPP is negative. If this should happen, it is plausible that the open peatland would shift from a slight C sink to a C source as global warming progresses. As the present peat accumulation rate is already low at the study site, the effect of an increase in decomposition rate will have considerable impact on C sequestration potential of the site, and of these types of peatlands in general. If there is an increase in total NPP, the question is whether NPP or decomposition would predominate. Enhanced tree growth might also lead to a major shift of C pool from peat to tree biomass. Clearly, further study is needed to more fully understand the future C sink–source role of hypermaritime peatlands in response to global warming.

Table 6. Mass loss (percentage loss of initial mass) of *Sphagnum fuscum* from litter bags in northern peatlands. Litters were incubated at the native habitat.

Location	Wetland type†	Used part	Drying preparation	Treatment after retrieval	Mesh size	Incubation depth	Mass loss		Source
							1 year	2 years	
Sweden (68°22' N, 19°03' E)	palsa mire	2 cm below capitula	oven dried (105°C)	-	1.0	0.5–5.5 cm below surface	5.4	-	Rosswall et al. (1975)
Sweden (57°10' N, 19°50' E)	raised bog	1.5 cm below capitula	air dried (22°C, at least 1 week)	cleaned with distilled water; fine roots removed with tweezers	0.2	10 cm below surface (oxic zone)	13.6	15.1	Johnson and Damman (1991)
Alberta (54°41' N, 113°28' W)	bog	aerial portion	oven dried (60°C, 24 h)	roots and debris removed with forceps	1.0	just below ground level	14.0	16.0‡	Szumigalski and Bayley (1996b)
British Columbia (54°13' N, 130°10' W)	sloping open peatland	2 cm below capitula	air dried over two weeks	cleaned with distilled water; fine roots removed with tweezers	0.2	10 cm below surface	18.1	20.1	this study
Manitoba (49°53' N, 95°54' W)	muskeg	green terminal portion minus capitula	-	-	1.0	0–5 cm below surface	1.7	-	Reader and Stewart (1972)
Manitoba (49°53' N, 95°54' W)	bog	green terminal portion minus capitula	-	-	1.0	0–5 cm below surface	0.1	-	Reader and Stewart (1972)
Ontario (49°40' N, 93°43' W)	poor fen	-	autoclaved, air dried (24–48 h)	cleaned without rinsing water	0.8	10 cm below surface (oxic zone)	12.0§	16.0¶	Rochefort et al. (1990)

† Terms from original sources were shown.

‡ Estimated from the graph.

§ 14 mo.

¶ 26 mo.

Table 7. Net primary production in *Sphagnum*-dominated northern peatlands.

Location	Wetland type†	Aboveground				Total	Belowground	Total	Source
		Moss	Herb	Shrub	Tree				
$\text{g m}^{-2} \text{yr}^{-1}$									
North America									
Alaska (64°52' N)	bog forest	–‡		74§	–	–	–	–	Luken et al. (1985)
Alaska (64°52' N)	bog	–		52§	–	–	–	–	Luken et al. (1985)
Québec (54°48' N, 66°49' W)	patterned fen	80–140		7–93§,¶	–	–	–	–	Moore (1989)
Québec (54°43' N, 66°42' W)	poor fen	38	27	49	0	114	–	–	Bartsch and Moore (1985)
Québec (54°43' N, 66°42' W)	transitional fen	39	90	47	0	176	–	–	Bartsch and Moore (1985)
Alberta (54°41' N, 113°28' W)	open bog	167	11	86	0	264	–	–	Szumigalski and Bayley (1996a)
Alberta (54°41' N, 113°28' W)	wooded bog	143	12	88	54	297	–	–	Szumigalski and Bayley (1996a)
Alberta (54°41' N, 113°28' W)	poor fen	123	54	134	0	310	–	–	Szumigalski and Bayley (1996a)
Alberta (54°41' N, 113°28' W)	bog	212	34	117	27	390	–	–	Thormann and Bayley (1997a)
British Columbia (54°13' N, 130°10' W)	sloping open peatland	140	29	2	3	175	20–82	195–257	this study#
Manitoba (49°53' N, 95°54' W)	muskeg	17	0	254	72	343	593	992††	Reader and Stewart (1972)
Manitoba (49°53' N, 95°54' W)	bog	55	0	316	0	371	1461	1942††	Reader and Stewart (1972)
Manitoba (49°53' N, 95°54' W)	bog forest	116	0	64	302	482	186	709††	Reader and Stewart (1972)
Minnesota (47–49° N, 92–95° W)	raised bog	320	14	200	99	633	–	–	Grigal (1991)
Minnesota (47°30' N, 93°30' W)	perched bog	380	22	42	314	758	–	–	Grigal (1991)
Minnesota (47° N, 92° W)	bog	247–313	10–26	37–73	0	322–389	95–190	486–546	Weltzin et al. (2000)‡‡
West Virginia (39°07' N, 79°35' W)	bog	451	208	386	0	1045	–	–	Wieder et al. (1989)
Europe and Russia									
Finland (61°02' N, 24°58' E)	raised bog	133§§	79¶¶	2	22	239	138	377	Vasander (1982)
Ireland	blanket bog	50	78	46	0	175	162	338	Doyle (1973)
England (54°65' N, 02°45' W)	blanket bog	35–213	67–394	5–258	0	388–802	99–228	487–902	Forrest and Smith (1975)##
England (54°40' N)	blanket mire	–	–	–	–	272	–	–	Bellamy et al. (1969)
Russia	mesotrophic forest bog	177		185§	246	608	–	–	Pjavchenko (1982)†††
Russia	oligotrophic forest bog	221		148§	95	464	–	–	Pjavchenko (1982)†††
Russia	mesotrophic bog	142‡‡‡	8	61	122	335	58	393	Bazilevich and Tishkov (1982)

† Terms from original sources were shown.

‡ Not reported.

§ Total for herbs and shrubs (Pjavchenko, 1982; Luken et al., 1985; Moore, 1989).

¶ 7, 41, and 93 g for pool, flark, and string, respectively (Moore, 1989).

Estimation excluding the area of bog woodland (9%) and assuming no production in the open pools (3%).

†† Including a 6% increment for consumption and secretion losses (Reader and Stewart, 1972).

‡‡ Data were taken in a mesocosm, and ranges are shown with minimum and maximum for the effects of water table and infrared loading manipulation (Weltzin et al., 2000).

§§ and ¶¶ Referred as “ground layer” and “field layer”, respectively (Vasander, 1982).

Ranges are shown with minimum and maximum among seven sites (Forrest and Smith, 1975).

††† Data might include belowground NPP (Pjavchenko, 1982).

‡‡‡ Including algae (Bazilevich and Tishkov, 1982).

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