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Spatial patterning of net primary production in wetlands of continental western Canada[1]

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Abstract: Net primary production in wetlands of continental western Canada (Alberta, Saskatchewan, Manitoba) is mapped and summarized by wetland type and ecoregion. The region contains 405 300 km^2 of wetlands, with peatlands representing 90.1% of all wetlands. Based on a regional synthesis of published values of net primary production, shrubby swamp and marsh wetlands produce more biomass annually through the process of net primary production than peatlands. Different peatland types appear to sequester similar amounts of plant biomass on an annual basis, with the exception of permafrost bogs that sequester less. Wetland net primary production for the region is calculated as 2.1×10^{14} g yr^{-1} of plant biomass, with 73.5% sequestered in peatlands. This is equivalent to 9.95×10^{13} g yr^{-1} of carbon. Provincially this carbon is partitioned into 50% for Manitoba, 30% for Alberta, and 20% for Saskatchewan. Over the last 1000 years, an average of only 5% of this biomass (and carbon) accumulate as peat, with most lost through the process of decomposition. When the annual amount of carbon that accumulates as peat is compared to the amount emitted provincially as anthropogenic greenhouse gases, wetlands present in each of the provinces accumulate 4% (Alberta), 8% (Saskatchewan), and 62% (Manitoba) of the emitted carbon annually. Wetlands in continental western Canada are a significant, active biosphere carbon sink following accumulation patterns of the last one thousand years. Future changes, particularly in fire frequency or intensity, may alter this accumulation pattern.
Keywords: wetlands, peatlands, net primary production, carbon.

Résumé : La production primaire nette des milieux humides de l'Alberta, de la Saskatchewan et du Manitoba à été cartographiée et répartie selon les types de milieux humides et les régions écologiques. Cette région de l'Ouest canadien contient 405 300 km^2 de milieux humides, dont 90,1 % sont des tourbières. Selon une synthèse régionale des valeurs publiées jusqu'à présent, les milieux marécageux arbustifs et les marais produisent chaque année, par les processus de production primaire nette, une plus grande biomasse que les tourbières. Les différents types de tourbières semblent accumuler des quantités similaires de biomasse végétale sur une base annuelle, à l'exception des tourbières à pergélisol qui en accumulent moins. La production primaire nette calculée pour les milieux humides de la région est de $2,1 \times 10^{14}$ g an^{-1} de biomasse végétale, dont 73,5 % est conservé dans les tourbières, ce qui correspond à $9,95 \times 10^{13}$ g an^{-1} de carbone. Ce carbone est partagé entre chaque province dans les proportions suivantes : 50 % pour le Manitoba, 30 % pour l'Alberta et 20 % pour la Saskatchewan. Au cours des 1000 dernières années seulement, une moyenne de 5 % de cette biomasse (et de ce carbone) s'est accumulée sous forme de tourbe, les pertes étant causées principalement par les processus de décomposition. En comparant les quantités annuelles de carbone s'accumulant sous forme de tourbe et les quantités de gaz à effet de serre d'origine anthropique émises, les milieux humides présents dans chaque province accumulent 4 % (Alberta), 8 % (Saskatchewan) et 62 % (Manitoba) du carbone émis annuellement. Selon les patrons d'accumulation des 1000 dernières années, les milieux humides de la partie continentale de l'Ouest canadien représentent donc un puits de carbone significatif et actif. Par contre, des changements futurs, notamment en ce qui concerne la fréquence ou l'intensité des feux, peuvent altérer ce patron d'accumulation.
Mots-clés : milieux humides, tourbières, production primaire nette, carbone.

Introduction

Where net primary production is greater than decomposition (in climates with a positive water balance and cool temperatures), wetlands accumulate peat and are thus net carbon sinks and important links in the global carbon cycle (Moore, Roulet & Waddington, 1998). Northern peatlands (fens and bogs) alone have been estimated to contain 4.55×10^{17} g of carbon – about one-third of the world's soil carbon (Gorham, 1991).

Canada is estimated to have the largest area of wetlands in the world – calculated between 1.27 to 1.7×10^{12} m^2 (13-17% of Canada's land area; National Wetlands Working Group, 1988; Gorham, 1991), and wetlands hold about 60% of all organic carbon in Canada as peat (Forestry Canada, 1992). Since Canada has such a large number of wetlands, the net budget of carbon fluxes between Canadian wetlands and the atmosphere has the potential to affect global carbon cycles. In continental western Canada (Alberta, Saskatchewan, and Manitoba), peatlands cover 365 157 km^2 and have accumulated 4.8×10^{16} grams of carbon, representing 2.1% of the world's terrestrial carbon in 0.25% of the landbase (Vitt *et al.*, 2000). We have previously estimated that over the long-term (the past 1000 years) peatlands (bogs and fens) in continental western Canada have accumulated and lost carbon at the rate of 33.4 g m^{-2} yr^{-1} and 14.0 g m^{-2} yr^{-1} respectively for a net carbon sink of 19.4 g m^{2} yr^{-1} (Vitt *et al.*, 2000). Non-peat accumulating wetlands (marshes and swamps) do accumulate some organic

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matter and hence carbon, however the amount of organic matter present is generally low (Zoltai, Siltanen & Johnson, 2000), and the rate at which this carbon accumulates is not known for continental western Canada, but is likely small when compared to peatlands. For these reasons, long-term carbon accumulation in non-peat accumulating wetlands is not included here.

Climate is a major factor affecting wetland development, form, and species composition (Damman, 1979; Glaser & Janssens, 1983; Halsey, Vitt & Zoltai, 1997). In the past, climatic changes have resulted in changes in wetland type at specific sites in western Canada (Vitt, Halsey & Zoltai, 1994) and elsewhere (Glaser & Janssens, 1983), and in shifts in their geographic distribution (Zoltai & Vitt, 1990; Halsey, Vitt & Gignac, 2000). Since carbon storage in wetlands is dependent on climatic regimes with a positive water balance and cool temperatures, global warming is expected to affect the geographic distribution of conditions suitable to wetland development and trigger shifts in wetland distribution and dynamics (Gignac & Vitt, 1994). These shifts have the potential to increase carbon storage or increase CO_2 flux to the atmosphere depending on the conditions. If realized, these climatic changes will results in greenhouse gas being released back into the atmosphere via increased decomposition (CO_2, CH_4) or fire (CO_2), as well as changes in plant annual production. The rate, magnitude, chemical species, and thresholds of future greenhouse gas sinks and sources through time and space will significantly affect Canada's future greenhouse gas budgets. A first step in understanding wetland carbon budgets is to determine where our current carbon is stored and how it is distributed spatially. The purpose of this paper is to provide a first assessment of the current carbon sequestered annually as plant biomass by total (above- and below-ground) net primary production of wetlands (both peatlands [bogs and fens] and non-peat accumulating wetlands [marshes and swamps]) as well as its spatial distribution. Additionally, long-term accumulation of peat in continental western Canada is evaluated relative to carbon emissions on a provincial basis.

Material and methods

WETLAND MAPPING

Aerial photography at a scale of 1:40 000 to 1:60 000 coupled with field verification was used to map wetlands in continental western Canada (Alberta, Saskatchewan, and Manitoba). Polygons were placed on 1:250 000 mylar base maps with the percent cover of specific wetland classes identified to the nearest 10% within an individual polygon, except for the Grassland Region of Alberta and Saskatchewan where cover values were estimated from those of the National Wetlands Working Group (1988). Since wetlands are only classified to the nearest 10% there is an inherent error in the methodology of 4%. Wetlands are classified as peatlands (permafrost bog and continental bogs without permafrost, and treed, shrubby, and open fens) and non-peat accumulating wetlands (marshes [open wetlands on shallow peat] and swamps [forested and shrubby wetlands on shallow peat]) (Vitt *et al.,* 2000). Distributions are presented by region (Arctic, Subarctic, Montane, Boreal, Parkland, and Grassland) modified for western Canada from the Ecological Stratification Working Group (1995) for Alberta by Strong and Thompson (1995).

NET PRIMARY PRODUCTION (NPP)

Above-ground net primary production values from wetlands in continental Canada and northern continental United States have been synthesized by individual species, vegetation layer (tree, shrub, herb, moss), and total amount (Campbell *et al.,* 2000; Table I). The amount of variation for above-ground NPP within wetland types is at least as large as between most wetland types (Campbell *et al.,* 2000). For wetland types that have standard deviations calculated, only pooled, total means for non-forested, non-peat accumulating wetlands (shrubby swamps and marshes) are significantly different from peatlands (Table I). For peatlands, pooled means are similar for all types, falling within the range of calculated standard deviations, with the exception of permafrost bogs that have a single, lower, total net primary production value.

Based on a literature synthesis, Campbell *et al.,* (2000) estimated total net primary production from above-ground net primary production (including the moss layer that has no below-ground component). Following a literature review, values of 50% and 30% of the above-ground net primary production (including moss layer) were considered reasonable estimates of below-ground net primary production (NPP) for peatlands and non-peat accumulating wetlands, respectively (Campbell *et al.,* 2000). These values are used here to estimate total above- and below-ground NPP from pooled above-ground NPP means for each wetland type (Table I). Site data for above-ground NPP was pooled by province/state to remove any bias from areas that were

TABLE I. Pooled means of above-ground net primary production by layer and site type (g m^{-2} yr^{-1}). Wetland types with missing layers are noted by an x. Standard deviations are calculated for wetland type where individual site data were available. The number of sites and/or years measured follows for each layer in brackets. Data are review in Campbell *et al.* (2000).

Wetland type	Tree above-ground	Shrub above-ground	Herb above-ground	Moss above-ground	Total above-ground	Total above- and below ground
Permafrost bog	77 (1)	no data	no data	24 (1)	176 (1)	264
Nonpermafrost bog	106 ± 192 (9)	247 ± 104 (12)	13 (10)	156 ± 157 (12)	449 ± 215 (11)	674
Wooded fen	44 (1)	108 (2)	64 (2)	74 (11)	358 (2)	537
Shrubby fen	x	63 (8)	125 (8)	118 (8)	263 (10)	395
Open fen	x	x	365 ± 458 (5)	163 (9)	268 ± 34 (4)	402
Wooded swamp	542 ± 279 (5)	31 ± 29 (5)	62 (4)	x	654 ± 197 (5)	850
Shrubby swamp	x	480 ± 260 (3)	727 ± 667 (3)	x	1232 ± 405 (3)	1602
Marsh	x	x	999 ± 529 (27)	x	1034 ± 456 (26)	1344

intensively sampled. Although some wetland types have statistically similar net primary production values, standard deviations cannot be calculated for all wetland types as original site data were not given in the literature (only study means were reported). Total above- and below-ground net primary production of wetlands in continental western Canada is estimated by utilizing the pooled mean values for each individual wetland type.

CARBON SEQUESTRATION, ACCUMULATION AND COMPARISON TO GREENHOUSE GAS EMISSONS

Carbon content of 393 wetland plants was determined using unpublished values from M. Thormann and S. Bayley, collected from sites representing all wetland types within continental western Canada. Mean carbon content of all wetland plants is 47.4 ± 5.3% of the dry weight. This conversion factor is used to determine the annual amount of carbon sequestered as plant biomass in wetlands through the process of net primary production at the provincial level.

The amount of annual carbon sequestration in peatlands for each of the provinces is determined from the long-term average accumulation and decomposition rates of 33.4 g m^{-2} yr^{-1} and 14.0 g m^{-2} yr^{-1} respectively for peat accumulating wetlands (Vitt *et al.,* 2000). As peatlands can flux both CO_2 and CH_4 to the atmosphere, and methane has an estimated greenhouse warming potential 21× that of CO_2 (IPCC 1996), the proportion of CO_2 and CH_4 emitted to the atmosphere via decomposition was estimated from the literature for different peatland types. Permafrost and nonpermafrost bogs that have thick, unsaturated acrotelms (mean of -38 cm calculated from Zoltai *et al.,* 2000) were assumed to flux only CO_2 to the atmosphere, with methane being oxidized in the acrotelm with negative values often reported (Vitt *et al*., 1990; Whiting, pers. comm., 2001). Open, patterned and nonpatterned graminoid and shrubby fens, with higher water tables (mean of -2 cm calculated from Zoltai *et al.,* 2000), have CO_2 to CH_4 flux ratios of 99:1 for continental western Canada (Turetsky *et al.,* 2001) with methane flux on the low end of other published values (reviewed in Turetsky *et al.,* 2001). Wooded fens have moderately thick, unsaturated acrotelms (-20 cm calculated from Zoltai *et al.,* 2000), and as such likely have flux ratios for CO_2 and CH_4 between those of bogs and wetter, open and shrubby fens, since some methane oxidation will occur.

The annual accumulation of carbon as plant biomass and flux as CO_2 and CH_4 in wetlands is compared to the amount of carbon emitted from greenhouse gases estimated for 1995 on a provincial basis for the three provinces in continental western Canada (Jaques, Neitzert & Boileau, 1997). Carbon based greenhouse gases include carbon dioxide, methane, hydrofluorocarbon, and perfluorocarbon generated from industrial processes that in the inventory included stationary and mobile fuel combustion, incineration, agriculture, prescribed burning, wastewater/compost, landfills, and anesthetics/propellants (Jaques, Neitzert & Boileau, 1997).

Results

WETLAND MAPPING

Wetlands occur over approximately 405 300 km^2 ± 16 200 (± 4%) of continental western Canada (Table II). Boreal and Subarctic Ecoregions contain the largest amount of peatland, while the Boreal Ecoregion has the largest amount of non-peat accumulating wetlands (Table II). Wetlands are most common in northern Alberta and Manitoba (Figure 1), forming part of two of the world's ten largest wetland complexes, the Mackenzie River Basin Peatland Complex (northern Alberta) and the Hudson Bay Lowland (northeastern Manitoba). Wetlands also dominate the landscape along the northern and northeastern shore of Lake Winnipeg, and eastward on the Canadian Shield.

NET PRIMARY PRODUCTION

Spatially, highest total net primary production of plant biomass in wetlands occurs along three oblique, parallel bands trending northwest to southeast (Figure 2). The southernmost band is represented by non-peat accumulating wetlands found in the southern uplands of Manitoba and extends westward along the northern edge of the Grasslands

TABLE II. Wetland distribution in continental western Canadian wetlands by type and ecoregions (km^2). Ecoregions are modified from those defined by the Ecological Stratification Working Group (1995) for Alberta following Strong and Thompson (1995). Percentages are based on total area (includes land and water). Values are considered accurate to ± 4%.

Type	Arctic	Subarctic	Montane	Boreal	Parkland	Grassland	Total	% Wetland
Permafrost bog	24	65 637	0	37 383	0	0	103 044	25.4
Nonpermafrost bog	0	1 841	1	29 112	4	0	30 958	7.6
Wooded fen	0	10 953	103	90 195	203	0	101 454	25.0
Shrubby nonpatterned fen	0	2 840	36	25 649	110	0	28 635	7.1
Open nonpatterned fen	253	30 337	48	36 614	189	0	67 441	16.7
Open patterned fen	0	4 139	64	29 179	8	0	33 390	8.2
Peatland	277	115 747	252	248 132	748	0	365 157	90.1
% Peatland	0.1	31.7	0.1	67.9	0.2	0	100.0	
Wooded swamp	0	23	0	1 249	8	0	1 280	0.3
Shrubby swamp	0	208	25	5 493	1 493	1 345	8 564	2.1
Marsh	52	890	27	14 530	7 683	7 157	30 339	7.5
Non-peat wetland	52	1 121	52	21 272	9 184	8 502	40 183	9.9
% Non-peat wetland	0.1	2.8	0.1	52.9	22.9	21.2	100.0	
Total wetland	329	116 868	304	269 403	9 932	8 502	405 339	100.0
% Total wetland	0.1	28.8	0.1	66.5	2.5	2.1	100.0	

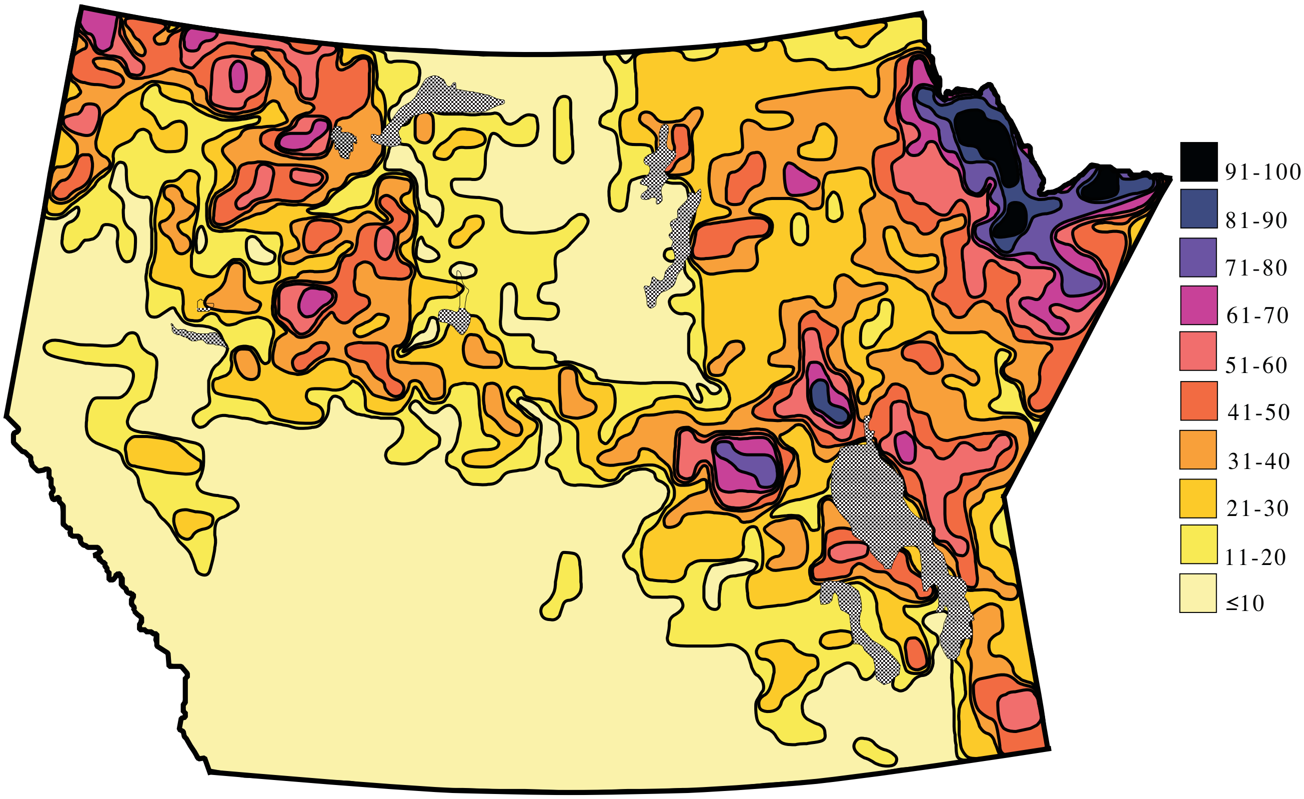

FIGURE 1. Distribution of wetlands in continental western Canada (Alberta, Saskatchewan, and Manitoba) in 10% increments based on total area (land + water). Data from Vitt *et al*. (1996) for Alberta excluding the Grasslands Region, Vitt and Halsey (unpubl. data) for Saskatchewan excluding the Grasslands Region, and Halsey, Vitt and Zoltai (1997) for Manitoba. Data for the Grasslands Region of Alberta and Saskatchewan were extracted from the National Wetlands Working Group (1988).

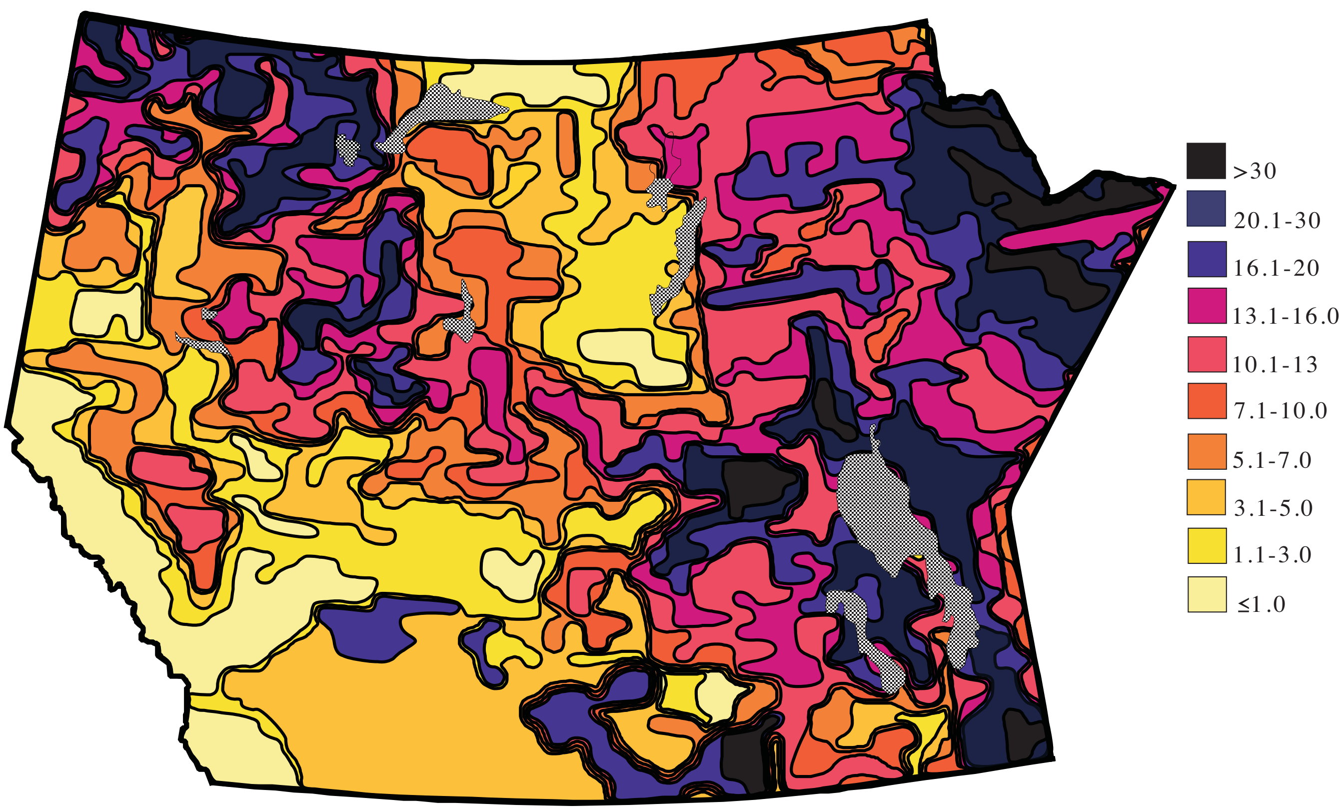

FIGURE 2. Annual amount of plant biomass generated by net primary production in g m^{-2} yr^{-1} for wetlands of continental western Canada.

Region. The central band includes peatlands of southeastern Manitoba and wetlands of the interlake area and extends along the northern and eastern shore of Lake Winnipeg to include the extensive fens of this area. In Saskatchewan the central band follows along the southern Boreal Region and into the Mackenzie River Basin Peatland Complex of northern Alberta, where peatlands are extensive. The third band of relatively high total net primary production parallels Hudson Bay in northeastern Manitoba and represents the peatlands of the Hudson Bay Lowland.

While peatlands represent about 90.1% of wetlands by cover, they account for only 73.5% of total above- and below-ground net primary production (Tables II and III), thus the distribution of NPP does not mimic wetland distribution. Decreases in total net primary production relative to cover are particularly noteworthy for permafrost bogs (Tables II and III). When ecoregion is considered, the Subarctic Region has less total net primary production relative to wetland cover, while the Grasslands Region has a greater amount of total net primary production relative to wetland cover (Tables II and III). Changes in percent cover can be attributed to the higher rate of total net primary production for open, non-peat accumulating wetlands relative to other wetland types, particularly for permafrost bogs. Wooded fens account for just over 25% of the total NPP for the region, while marshes account for 20%. Continental bogs without permafrost, highly valued for horticultural peat extraction, account for only 10% of the total NPP, whereas the climatically sensitive permafrost bogs account for 13% of total NPP. As NPP measurements are highly variable even between years at individual sites (Campbell *et al.,* 2000) with standard deviations often greater than 50% where sufficient data exist (Table I), the values presented here should be viewed in terms of their magnitude and proportions between types.

CARBON SEQUESTRATION AND ACCUMULATION

Wetlands of continental western Canada sequester 9.95×10^{13} g yr^{-1} of carbon as plant biomass through the process of net primary production. Plant biomass in Manitoba wetlands contain half of this carbon, with wetland plant biomass in Alberta and Saskatchewan containing 30% and 20%, respectively. Only a fraction of this carbon (average 5% or 4.58 x 10^{12} g yr^{-1}) is placed into long-term storage through the process of peat accumulation, with the majority being returned back to the atmosphere by either aerobic (CO_2) or anaerobic (CH_4) decomposition. Over a long-time interval (1000 years), bogs and fens have been estimated to accumulate and decay 33.4 g m^{-2} yr^{-1} and 14.0 g m^{-2} yr^{-1} of carbon, respectively, in continental western Canada (Vitt *et al.,* 2000). While some peatland types and climatic regions have been shown to have different long-term net peat accumulation rates in other areas (Tolonen & Turunen, 1996; Robinson & Moore, 1999; 2000), we currently do not have sufficient data to determine peat accumulation rates by peatland types for continental western Canada. According to these numbers, as well as the CO_2 and CH_4 flux ratios for the different peatland types, peatlands in continental western Canada have been acting as carbon sinks over the last 1000 years, accumulating 4.58×10^{12} g yr^{-1} (Table VI)

When the long-term, annual accumulation of carbon as peat in wetlands is compared to the amount of carbon emitted from anthropogenic greenhouse gases in 1995 (Jaques, Neitzert & Boileau, 1997) (Table IV), carbon accumulation in peat offsets emission by about 4% (Alberta), 8% (Saskatchewan), and 62% (Manitoba), or 8% for the three prairie provinces.

It is important to note that the long-term (1000 years) carbon accumulation and decompostion rates extracted from Vitt *et al*. (2000) are based on peat stratigraphies taken from across continental western Canada, and as such will include carbon removal from fires that occurred over the 1000-year time period. It has been suggested, however, that fire frequency/intensity will increase in continental western Canada with climate warming (Starfield & Chapin, 1996; Stocks *et al.,* 1998), and thus the amount of carbon removed from combustion of peat may also increase substantially.

Discussion

Based on net primary production values obtained from the published literature, wetland coverage in western continental Canada, and a carbon conversion factor derived from wetland species carbon values, the annual amount of

TABLE III. Total net primary production in wetlands of continental western Canada by wetland type and ecoregion (g yr^{-1}). Ecoregions are modified from those defined by the Ecological Stratification Working Group (1995) for Alberta following Strong and Thompson (1995)

Type	Arctic	Subarctic	Montane	Boreal	Parkland	Grassland	Total	% Wetland
Permafrost bog	6.34×10^{09}	1.73×10^{13}	0	9.87×10^{12}	0	0	2.72×10^{13}	13.0
Nonpermafrost bog	0	1.24×10^{12}	6.74×10^{08}	1.96×10^{13}	2.69×10^{09}	0	2.08×10^{13}	9.9
Wooded fen	0	5.88×10^{12}	5.53×10^{10}	4.84×10^{13}	1.09×10^{11}	0	5.44×10^{13}	25.9
Shrubby nonpatterned fen	0	1.12×10^{12}	1.42×10^{10}	1.01×10^{13}	4.34×10^{10}	0	1.13×10^{13}	5.4
Open nonpatterned fen	1.02×10^{11}	1.22×10^{13}	1.93×10^{10}	1.47×10^{13}	7.60×10^{10}	0	2.71×10^{13}	12.9
Open patterned fen	0	1.66×10^{12}	2.57×10^{10}	1.17×10^{13}	3.22×10^{09}	0	1.34×10^{13}	6.4
Peatland	1.08×10^{11}	3.94×10^{13}	9.75×10^{10}	1.14×10^{14}	2.34×10^{11}	0	1.54×10^{14}	73.5
% Peatland	0.1	25.6	0.1	74.0	0.2	0.0	100.0	
Wooded swamp	0	1.96×10^{10}	0	1.06×10^{12}	6.80×10^{09}	0	1.09×10^{12}	0.5
Shrubby swamp	0	3.33×10^{11}	4.01×10^{10}	8.80×10^{12}	2.39×10^{12}	2.15×10^{12}	1.37×10^{13}	6.4
Marsh	6.99×10^{10}	1.20×10^{12}	3.63×10^{10}	1.95×10^{13}	1.03×10^{13}	9.62×10^{12}	4.07×10^{13}	19.6
Non-peat wetland	6.99×10^{10}	1.55×10^{12}	7.64×10^{10}	2.94×10^{13}	1.27×10^{13}	1.17×10^{13}	5.55×10^{13}	26.5
% Non-peat wetland	0.1	2.8	0.1	53.0	22.9	21.1	100.0	
Total wetland	1.78×10^{11}	4.10×10^{13}	1.74×10^{11}	1.43×10^{14}	1.29×10^{13}	2.35×10^{13}	2.10×10^{14}	100.0
% Total wetland	0.1	19.6	0.1	68.4	6.1	5.6	100.0	

TABLE IV. Yearly, long-term budgets of carbon accumulation in peatlands of continental western Canada. Long-term accumulation and decomposition rates follow those of Vitt *et al.* (2000). Total flux has been converted to CO_2 equivalents following a greenhouse warming potential for methane of 21× that of carbon dioxide (IPCC, 1996). Carbon emitted from anthropogenic sources is also reported in CO_2 equivalents (Jaques, Neitzert & Boileau, 1997).

Type	Alberta	Saskatchewan	Manitoba	Total
Permafrost bog	6.84×10^{11}	1.40×10^{11}	2.62×10^{12}	3.44×10^{12}
Nonpermafrost bog	3.66×10^{11}	2.55×10^{11}	4.13×10^{11}	1.03×10^{12}
Wooded fen	1.19×10^{12}	6.64×10^{11}	1.54×10^{12}	3.39×10^{12}
Shrubby nonpatterned fen	3.96×10^{11}	1.76×10^{11}	3.84×10^{11}	9.56×10^{11}
Open nonpatterned fen	6.58×10^{11}	2.68×10^{11}	1.33×10^{12}	2.25×10^{12}
Open patterned fen	1.56×10^{11}	2.01×10^{11}	7.59×10^{11}	1.12×10^{12}
Peatland	3.45×10^{12}	1.70×10^{12}	7.04×10^{12}	1.22×10^{13}
Carbon emitted from catotelm	1.85×10^{12}	9.07×10^{11}	3.85×10^{12}	7.08×10^{12}
Carbon budget	1.60×10^{12}	7.93×10^{11}	2.19×10^{12}	4.58×10^{12}
Carbon emitted (anthropogenic)	4.24×10^{13}	1.03×10^{13}	3.55×10^{12}	5.63×10^{13}
% Wetland offset	3.8	7.7	61.7	8.1

carbon sequestered as plant biomass in wetlands is 2.10×10^{14} g yr ^{1}. Since total net primary production differs for different wetland types, the distribution of carbon sequestered as plant biomass does not follow the distribution of wetlands. While peatlands represent 90.1% of wetlands in the area, they only account for 73.5% of the total net primary production, with total net primary production being relatively low in the Subarctic Region and relatively high in the Aspen Parkland and Grasslands Regions. This difference can be attributed to the low net primary production of permafrost bogs that dominate the Subarctic Region and the relatively high net primary production of shrubby swamps and marshes that dominate the Aspen Parkland and Grasslands Region. Long-term peat accumulation represents about 5% of carbon sequestered annually as plant biomass. Hence wetlands in continental western Canada represent a significant active biosphere carbon sink.

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Literature cited

Campbell, C. D., D. H. Vitt, L. A. Halsey, I. Campbell, M. N. Thormann & S. E. Bayley, 2000. Net primary production and standing biomass in wetland in boreal Canada. NOR-X-369. Northern Forestry Centre, Canadian Forest Service, Edmonton, Alberta.

Damman, A. W. H., 1979. Geographic patterns in peatland development in eastern North America. In Proceedings of the International Symposium of Classification of Peat and Peatlands, International Peat Society. Hyytiala, Finland.

Ecological Stratification Working Group, 1995. Terrestrial ecozones, ecoregions, and ecodistricts of Canada: Provinces of Alberta, Saskatchewan, and Manitoba. A national ecological framework for Canada. Agriculture and Agri-Foods Canada, Research Centre for Land and Biological Resources Research and Environment Canada, State of Environment Directorate, Ottawa, Ontario.

Forestry Canada, 1992. The State of Canada's Forests. Canadian Forest Service, Ottawa, Ontario.

Glaser, P. H. & J. A. Janssens, 1983. Raised bogs in eastern North America: Transitions in landforms and gross stratigraphy. Canadian Journal of Botany, 64: 395-415.

Gignac, L. D. & D. H. Vitt, 1994. Responses of northern peatlands to climate change: Effects on byrophytes. Journal of the Hattori Botanical Laboratory, 75: 119-132.

Gorham, E., 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. Ecological Applications, 1: 182-512.

Halsey, L. A., D. H. Vitt & L. D. Gignac, 2000. *Sphagnum*-dominated peatlands in North America since the last glacial maximum: Their occurrence and extent. The Bryologist, 103: 334-352.

Halsey, L. A., D. H. Vitt & S. C. Zoltai, 1997. Climatic and physiographic controls on wetland type and distribution in Manitoba, Canada. Wetlands, 17: 243-262.

Jaques, A., F. Neitzert & P. Boileau, 1997. Trends in Canada's Greenhouse Gas Emissions (1990-1995). Environment Canada, Ottawa, Ontario.

Moore, T. R., N. T. Roulet & J. M. Waddington, 1998. Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. Climatic Change, 40: 229-245.

National Wetlands Working Group, 1988. Wetlands of Canada. Ecological Land Classification Series No. 24. Sustainable Development Branch, Environment Canada, Ottawa and Polyscience Publications, Montréal, Québec.

Robinson, S. D. & T. R. Moore, 1999. Carbon and peat accumulation over the past 1200 years in a landscape with discontinuous permafrost, northwestern Canada. Global Biogeochemical Cycles, 13: 591-601.

Robinson, S. D. & T. R. Moore, 2000. The influence of permafrost and fire upon carbon accumulation in High Boreal Peatlands, Northwest Territories, Canada. Arctic, Antarctic, and Alpine Research, 32: 155-166.

Starfield, A. M., & F. S. Chapin, 1996. Model of transient changes in arctic and boreal vegetation in response to climate and land use change. Ecological Applications, 6: 842-864.

Stocks, B. J., M. A. Fosberg, T. J. Lynham, L. Mearns, B. M. Wotton, B. M. Yang, J. Z. Jin, K. Lawrence, G. R. Hartley, J. A. Mason, and D. W. McKenney, 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. Climatic Change, 38: 1-13.

Strong, W. L. & J. M. Thompson, 1995. An attribute database for a 1:1 000 000 scale ecodistrict classification of Alberta based on natural subregions and nationally recognized ecodistricts. Alberta Environmental Protection, Edmonton, Alberta.

Tolonen, K. & Turunen, 1996. Accumulation rates of carbon in mires in Finland and implications for climate change. Holocene, 6: 171-178.

Turetsky, M., K. Wieder & D. H. Vitt, 2001. Boreal peatland carbon fluxes under varying permafrost regimes. Soil Biology and Biochemistry: in press.

Vitt, D., S. Bayley, T. Jin, L. Halsey, B. Parker & R. Craik, 1990. Methane and carbon dioxide production from wetlands in boreal Alberta. Report on Contract No. 90-0270 to Alberta Environment, 35 p.

Vitt, D. H., L. A. Halsey, I. E. Bauer & C. Campbell, 2000. Spatial and temporal trends in carbon sequestration in peatlands of continental western Canada through the Holocene. Canadian Journal of Earth Sciences, 37: 683-693.

Vitt, D. H., L. A. Halsey, M. N. Thormann & T. Martin, 1996. Peatland inventory of Alberta Phase 1: Overview of peatland resources in the Natural Regions and Subregions of the province. National Centres of Excellence in Sustainable Forest Management, Edmonton, Alberta.

Vitt, D. H., L. A. Halsey & S. C. Zoltai, 1994. The bog landforms of continental western Canada, relative to climate and permafrost patterns. Arctic and Alpine Research, 26: 1-13.

Zoltai, S. C. & D. H. Vitt, 1990. Holocene climatic change and the distribution of peatlands in western interior Canada. Quarternary Research, 33: 231-240.

Zoltai, S. C., R. M. Siltanen & J. D. Johnson, 2000. A wetland environmental data base. NOR-X Report, Northern Forestry Centre, Canadian Forest Service, Edmonton, Alberta.