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Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands

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Abstract. We analyzed the relationship between net ecosystem exchange of carbon dioxide (NEE) and irradiance (as photosynthetic photon flux density or PPFD), using published and unpublished data that have been collected during midgrowing season for carbon balance studies at seven peatlands in North America and Europe. NEE measurements included both eddy-correlation tower and clear, static chamber methods, which gave very similar results. Data were analyzed by site, as aggregated data sets by peatland type (bog, poor fen, rich fen, and all fens) and as a single aggregated data set for all peatlands. In all cases, a fit with a rectangular hyperbola ($NEE = \alpha\, PPFD\, P_{max}/(\alpha\, PPFD + P_{max}) + R$) better described the NEE-PPFD relationship than did a linear fit ($NEE = \beta\, PPFD + R$). Poor and rich fens generally had similar NEE-PPFD relationships, while bogs had lower respiration rates ($R = -2.0$ μmol m^{-2} s^{-1} for bogs and -2.7 μmol m^{-2} s^{-1} for fens) and lower NEE at moderate and high light levels ($P_{max} = 5.2$ μmol m^{-2} s^{-1} for bogs and 10.8 μmol m^{-2} s^{-1} for fens). As a single class, northern peatlands had much smaller ecosystem respiration ($R = -2.4$ μmol m^{-2} s^{-1}) and NEE rates ($\alpha = 0.020$ and $P_{max} = 9.2$ μmol m^{-2} s^{-1}) than the upland ecosystems (closed canopy forest, grassland, and cropland) summarized by *Ruimy et al.* [1995]. Despite this low productivity, northern peatland soil carbon pools are generally 5-50 times larger than upland ecosystems because of slow rates of decomposition caused by litter quality and anaerobic, cold soils.

1. Introduction

Northern peatlands play a unique role in the terrestrial carbon cycle. Although the aboveground net primary productivity (ANPP) of northern peatlands is lower than the ANPP of other northern ecosystems because of saturated conditions and lower concentrations of essential nutrients [e.g. *Damman and French* 1987; *Glaser*, 1987; *Grigal et al.*, 1985], long-term peatland carbon accumulation rates (29 g C m^{-2} yr^{-1}; [*Gorham*, 1991]) are roughly 10 times larger than

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mean, long-term (millennial) soil carbon accumulation rates for upland ecosystem soils [*Schlesinger*, 1990]. Northern peatlands contain roughly 450 Gt C in peat, about one-third of the total world pool of soil carbon [*Gorham*, 1991]. Northern peatlands are often spatially small (frequently smaller than 1 km^2) and thus are often ignored in regional- and global-scale ecosystem and climate models that do not resolve surface classes of this size. For example, *Melillo et al.*, [1993] ignore wetlands in their global carbon response to climate change and elevated CO_2. When aggregated, however, northern peatlands are areally extensive. Boreal and subarctic peatlands cover about 3.5 million km^2 [*Gorham*, 1991]. Much of the boreal region in Canada has >25% peatland cover, and the Hudson Bay lowlands in Canada and the peat basin of western Siberia are immense tracts of land where more than 50% of the landscape is peatland [*National Wetlands Working Group*, 1988; *Gorham*, 1991].

Peatlands have not received much attention in ecosystem models developed for global-scale carbon analyses. Many of these global carbon models use broad ecosystem classifications to characterize the landscape, with different ecophysiological parameters for their vegetation classes. In one commonly used, global vegetation classification scheme [*Matthews*, 1983] northern peatlands fall within two classes, 'arctic and alpine tundra, mossy bog' and 'temperate/sub-polar evergreen needle-leaved forest'. Generally, these global models calculate plant productivity as a function of photosynthetically active radiation (PAR) and other variables

(e.g., CASA [*Potter et al.*, 1993]; Frankfurt Biosphere Model (FBM) [*Kindermann et al.*, 1996]; Biome-BGC [*Running and Coughlan*, 1988]; TEM [*Raich et al.*, 1991]; TURC [*Ruimy et al.*, 1996]; BIOME3 [*Haxeltine and Prentice*, 1996]. This functional relationship between PAR and productivity can be linear for production efficiency models (e.g., CASA) or nonlinear for more ecophysiological models (e.g., TEM, FBM, Biome-BGC, and BIOME3). Parameters for these relationships have been derived from data for upland ecosystems but have not been evaluated for peatlands.

In their review of simultaneous, instantaneous measurements of net ecosystem exchange of carbon dioxide (NEE) and PAR, *Ruimy et al.* [1995] compiled 126 published data sets from a range of terrestrial ecosystems (broadleaf forest, conifer forest, C_3 grassland, C_4 grassland, C_3 crops, C_4 crops, and mixed vegetation), but included no data from northern peatlands. Recently, *Whiting* [1994] reported NEE-PAR data for peatland sites in the Hudson Bay Lowlands, *Shurpali et al.* [1995] reported NEE-PAR data for a peatland in Minnesota, and *Waddington and Roulet* [1996] and *Alm et al.* [1997] reported NEE-PAR data for peatlands in Scandinavia. In this paper we extend the analysis of the relationship between irradiance and ecosystem productivity of *Ruimy et al.* [1995] to northern peatlands, using a number of independently collected data sets from North America and Europe [*Whiting*, 1994; *Waddington and Roulet*, 1996; *Carroll and Crill*, 1997; *Suyker et al.*, 1997; *Lafleur et al.*, 1997; *Ball*, 1996; *Bhardwaj*, 1997; J.L. Bubier et al., Controls on net ecosystem CO2 exchange in a boreal peatland complex, submitted to *Global Biogeochem. Cycles*, 1997, (hereinafter referred to as Bubier et al., submitted manuscript, 1997); and L.M. Bellisario et al., Net ecosystem exchange of CO_2 in a boreal peatland, Manitoba, Canada, submitted to *Ecoscience*, 1997, (hereinafter referred to as Bellisario et al., submitted manuscript, 1997)]. We (1) develop linear and curvilinear relationships between photosynthetic photon flux density (PPFD) and NEE for northern peatlands, (2) explore differences between peatland classes (bog, poor fen, and rich fen), and (3) compare these results to the aggregated forest, grassland, and cropland relationships developed by Ruimy et al. [1995].

These data and analyses can contribute to improved characterization of northern peatlands in general ecosystem models. Global-scale models will be able to use the relationships developed to help parameterize a peatland ecosystem class with characteristics distinct from those of upland ecosystem classes. This work can also contribute to the development of a peatland ecosystem model; such a model could be used to extrapolate measured peatland carbon fluxes to the northern landscape and also to explore the sensitivity of peatland carbon balances to climate variability and change.

2. Site Descriptions

NEE-PAR data were collected from six peatland sites in North America and one site in Sweden (Table 1). These sites span a range of peatland classes (bog, poor fen, and rich fen) and vegetation types, as well as a climate gradient from cool temperate (New Hampshire) to cold boreal (Hudson Bay lowlands) (Table 1). Bogs are acidic, *Sphagnum*-dominated peatlands, which are unaffected by nutrient-rich groundwater

from surrounding mineral soils [*National Wetlands Working Group*, 1988]. The bogs in this study have pore water pH values of 3.9-4.8, are dominated by *Sphagnum* species and ericaceous shrubs, and have well-defined microtopography. Rich fens are nutrient-rich peatlands, minerotrophic from groundwater influence with a water table near or above the peat surface. The pH of rich fens in this study ranges from 6.5 to 7.1. They are dominated by "brown" mosses (Amblystegiaceae family) in the bryophyte layer and either by sedges or shrubs in the vascular plant component of the ecosystem. Poor fens are intermediate peatlands because they have groundwater influence, but are more acidic than rich fens and are *Sphagnum*-dominated in the moss layer [*Gorham and Janssens*, 1992]. In this study, the pH of poor fens ranges from 4.5 to 5.8, but all are dominated by *Sphagnum* and *Carex* species. All the sites in this study are open (<10% tree cover) with low shrubs or sedges, or treed (10-25% tree cover). Forested peatlands (closed canopy tree cover > 5 m) also occur in the boreal and temperate zones [*Zoltai and Martikainen*, 1996] and may have a different NEE-PPFD response than those described here.

2.1. SITE 1: Northern Study Area (NSA) Boreal Ecosystem-Atmosphere Study (BOREAS) Peatland Complex, Manitoba

The peatland complex is located 50 km west of Thompson, Manitoba and was one of the tower sites in the BOREAS NSA. The site occurs in the zone of discontinuous permafrost and contains frozen peat plateaus, unfrozen fens, and permafrost collapse scar bogs and fens (Bubier et al., submitted manuscript, 1997). A flux tower was located in center of the rich fen, an unfrozen, open and treed mixed-shrub fen [*Lafleur et al.*, 1997]. Chamber measurements were conducted in four areas of the peatland, including collapse scar bog and fen, poor fen, and rich fen (Bubier et al., submitted manuscript, 1997; Bellisario et al., submitted manuscript, 1997). These sites were chosen for their wide range of vegetation, from treed to sedge-dominated, *Sphagnum* to brown moss, and pH ranges from 4.1 to 7.0.

2.2. SITE 2: Southern Study Area (SSA) BOREAS Fen, Saskatchewan

The SSA fen is located 115 km northeast of Prince Albert, Saskatchewan, and was one of the tower sites for the southern study area of BOREAS. The peatland is a rich fen with some patterning of strings and pools [*Suyker et al.*, 1996; 1997]. The water table is generally at or above the peat surface during the growing season. Vegetation is dominated by dwarf birch (*Betula pumila* L.), buckbean (*Menyanthes trifoliata* L.), brown mosses (e.g., *Drepanocladus* spp.), and dense stands of *Carex* spp.

2.3. SITE 3: Frontenac Bog, Quebec

This peatland is located in Le Parc Regionale de Frontenac, near Thetford Mines, Quebec. The bog is raised with a domed profile and has distinct microtopographic development of hummocks, lawns, strings, and pools [*Ball*, 1996]. The vegetation on the hummocks and drier, raised areas is dominated by stunted black spruce trees (*Picea mariana* (Mill.)

Table 1. Site Locations and Descriptions

Site	Name	Location	Mean JJA Temperature	Peatland Type[a]	pH	Major Species[b]
1a	BOREAS NSA fen	Thompson, Manitoba, Canada NSA peatland, 55°55'N, 98°25'W	13.9	OlsB	4.1	Chamaedaphne calyculata, Sphagnum fuscum
1b				OgB	4.2	Carex limosa, Sphagnum riparium
1c				OgPF	4.5	Carex aquatilis, Sphagnum riparium
1d				OgPF	5.8	Carex rostrata, Sphagnum riparium
1e				TmsF	7.0	Larix laricina, Betula glandulosa, Carex spp., Menyanthes trifoliata, Scorpidium scorpioides
2	BOREAS SSA fen	Candle Lake, Saskatchewan, Canada, SSA peatland, 53°57'N, 105°57'W	14.5	OgF	7.1	Carex lasiocarpa, Betula pumila, Menyanthes trifoliata, Drepanocladus spp.
3a	Frontenac Bog	Frontenac Park, Thetford Mines, Quebec, Canada, 46°35'N, 72°31'W	15.8	TmsB	NA	Picea mariana,Ledum groenlandicum, Sphagnum fuscum
3b				OlsB	NA	Chamaedaphne calyculata, Sphagnum rubellum
3c				OgB	NA	Rhynchospora alba, Sphagnum papillosum
4a	Stor-Åmyran	Umeå, Sweden, 63°44'N, 20°06'E	13.9	OlsB	4.6	Rubus chamaemorus, Sphagnum fuscum
4b				OgB	4.5	Eriophorum vaginatum, Sphagnum balticum
4c				OgB	4.3	Eriophorum vaginatum, Sphagnum majus
5	Sallie's Fen	Barrington New Hampshire, United States, 43°12'N, 71°03'W	19.8	OmsPF	5.1	Chamaedaphne calyculata, Carex rostrata Sphagnum magellanicum
6a	Lake 632	Experimental Lakes Area Kenora, Ontario, Canada, 49°45'N, 94°30'W	16.4	TmsB	4.3	Picea mariana, Chamaedaphne calyculata, Sphagnum fuscum
6b				OlsB	4.5	Chamaedaphne calyculata, Sphagnum angustifolium
6c				OgB	4.8	Carex oligosperma, Sphagnum fallax
6d				OgPF	5.1	Carex limosa, Sphagnum fallax/S. majus
7a	Hudson Bay lowland	Moosonee, Ontario, Canada, 51°33'N, 81°07'W	13.8	OgF	6.8	Carex spp., Scirpus spp., Equisetum spp. Scorpidium scorpioides
7b				OgF	6.5	Carex spp., Scirpus spp., Menyanthes trifoliata
7c				OlsB	4.1	Picea mariana, Ledum groenlandicum, Sphagnum fuscum, S. rubellum, Cladina spp.

Site references are as follows: site 1 (chamber), *Bellisario* [1996], Bellisario et al. (submitted manuscript, 1997), Bubier et al. (submitted manuscript, 1997), site 1 (tower), *Lafleur et al.* [1997]; site 2: *Suyker et al.* [1997]; site 3: *Ball* [1996]; site 4: *Waddington and Roulet* [1996]; site 5: *Carroll and Crill* [1997]; site 6: *Bhardwaj* [1997]; and site 7: *Whiting* [1994]. Abbreviations are as follows: JJA, June, July, and August; NA, not available.

[a] Peatland type abbreviations are as follows: O, open; T, treed; g, graminoid; ls, low shrub; ms, mixed shrub; B, bog; PF, poor fen; F, rich fen [*National Wetlands Working Group*, 1988, pp. 416-427].

[b] Nomenclature follows *Fernald* [1950] for vascular plants, *Anderson et al.* [1990] for mosses, and *Anderson* [1990] for *Sphagnum* spp.

BSP.) and ericaceous shrubs, while the lawns and pools have more sedge cover. The bryophyte layer is composed entirely of *Sphagnum* mosses.

2.4. SITE 4: Stor-Åmyran Peatland, Sweden

Stor-Åmyran is a raised bog about 15 km south of Umeå, Sweden. As a raised bog, it has well-developed ridges and pools with smaller microtopographic features of hummocks and hollows [*Waddington and Roulet*, 1996]. The vegetation is composed primarily of *Sphagnum* mosses, ericaceous shrubs, and some herbaceous species (*Eriophorum vaginatum* and *Rubus chamaemorous* L.).

2.5. SITE 5 - Sallie's Fen, New Hampshire

This peatland is a small, minerotrophic poor fen, located in southeast New Hampshire near the town of Barrington. The vegetation is dominated by sedges (*Carex rostrata* Stokes), shrubs (*Chamaedaphne calyculata* (L.) Moensch and *Vaccinium* spp.), and *Sphagnum* mosses [*Frolking and Crill*, 1994; *Carroll and Crill*, 1997].

2.6. SITE 6: Lake 632, Experimental Lakes Area, Ontario

Lake 632, is a small bog in the Experimental Lakes Area near Kenora, Ontario. Vegetation is dominated by stunted trees (*Picea mariana*) and shrubs (*Ledum groenlandicum* Oeder and *Chamaedaphne calyculata*) in the drier areas and by sedges (*Carex* spp.) in the wetter hollows and pond margin. The bryophyte layer is composed entirely of *Sphagnum* mosses (J.L. Bubier, unpublished data, 1995).

2.7. Site 7: Hudson Bay Lowlands, Ontario

The peatlands in this study area are located along a successional gradient from a coastal fen (youngest) to interior fen to bog (oldest) [*Whiting*, 1994]. Both fens are dominated by the brown moss *Scorpidium scorpioides* (Hedw.) Limpr. in the wettest locations. The fen vascular plant communities are composed of sedges (*Carex* spp. and *Scirpus* spp.), horsetail (*Equisetum* spp.), and buckbean (*Menyanthes trifoliata*). With the exception of degrading pools, the interior bog is drier than the fens. Bog plant communities are characterized by lichen (*Cladina* spp.), ericaceous shrubs and *Sphagnum* mosses.

3. Data Sets

Net ecosystem exchange of CO_2 (NEE) was measured by a variety of clear chamber techniques in six of the seven study sites and by eddy-covariance instruments mounted on a micrometeorological tower at two of the sites. All of the chamber studies used clear, closed chambers placed into collars that were inserted into the peat to prevent disturbance and to create an airtight seal. Some form of climate-control system was used in all but one of the studies to minimize changes in air temperature and relative humidity inside the chamber during the sampling period. Closed-path CO_2 sensors (infrared gas analyzers) measured the changes in CO_2 concentration within the chambers. The methodology is described in detail by *Whiting et al.* [1992]. In the chamber studies,

photosynthetically active radiation (PAR) was measured with a small PAR sensor placed on top of the chamber during the sampling period. Measurements were generally taken as a set, with full light (clear chamber), fractional light (shrouded chamber), and dark (opaque shroud). Clear and partially shrouded chambers measured the net flux of CO_2 due to both photosynthesis and autotrophic and heterotrophic respiration. Chambers with opaque shrouds (PPFD = 0) measured total respiration. We adopted a sign convention of carbon uptake or productivity as positive NEE and respiration as negative NEE. Chamber measurements were made within a couple of hours of local noon (generally on sunny days), so incident radiation levels were generally high (~1000-2000 μmol m^{-2} s^{-1}). For specific details for each site, see the references listed in Table 1. All NEE values are reported in μmol CO_2 m^{-2} s^{-1}.

At the two tower sites, carbon dioxide flux was measured using the eddy-correlation technique [e.g., *Businger*, 1986]. A sonic anemometer, a fine wire thermocouple, a Krypton hygrometer, and a closed-path CO_2 sensor were used to measure fluctuations of wind speed, temperature, humidity, and carbon dioxide concentration. Mean air temperature, humidity, horizontal wind speed and PAR (photosynthetically active radiation) were also measured. For specific details for these sites, see *Lafleur et al.* [1997] and *Suyker et al.* [1997]. Tower measurements were made every half hour throughout the growing season, so dark measurements were made at night, low-light measurements were made in the morning and evening, and high-light measurements were made in the middle of the day.

4. Data Analysis

4.1. Radiation

Photosynthetically active radiation (PAR) was reported by some groups as PAR (W m^{-2}) and by some groups as photosynthetic photon flux density (PPFD) (μmol m^{-2} s^{-1} of photons with wavelengths of 0.4-0.7 μm). We converted all values to PPFD using 1.0 W m^{-2} PAR equals 4.6 μmol m^{-2} s^{-1} [*Ruimy et al.*, 1995]. Photosynthetic radiation can be measured as incident, intercepted (by plant tissue), or absorbed (not reflected by plant tissue). As peatland vegetation generally creates a complete ground cover (i.e., there is no bare "soil"), all incident radiation that is not reflected from standing water will be intercepted by vegetation. The euphotoic zone in *Sphagnum* (within which all but 1% of incident light is absorbed) ranges from about 1 to 5 cm [*Clymo and Hayward*, 1982]. The mosses are green as far down as adequate light will penetrate, so we assumed that all nonreflected PAR was absorbed by plant tissue (which would be green and photosynthesizing during the midseason). All sites in this study with chamber measurements reported incident PPFD, while tower measurements included incident and reflected PPFD. For the tower at the NSA BOREAS fen complex (site 1), reflected PPFD averaged 5.5±1.1% of incident PPFD (mean and standard deviation of observations with incident PPFD > 50 μmol m^{-2} s^{-1} and reflected PPFD >0 μmol m^{-2} s^{-1}; n = 1992). Since the observed PAR albedo for peatlands was this small, we follow *Ruimy et al.* [1995] and consider all chamber radiation measurements to be equivalent to absorbed radiation.

4.2.   Seasonality

Data collection at most of the sites began before or soon after snowmelt and thaw and often continued well into the fall and early winter. As would be expected, plant photosynthetic activity was frequently reduced in spring and fall because of limitations other than low light levels (e.g., air and/or plant temperature, phenology and recovery from winter dormancy [e.g., *Larcher*, 1993], and frozen or dry soils limiting water availability). In order to develop an NEE-PPFD relationship that was minimally influenced by these early- and late-season limitations, we divided the data into three groups: early, middle, and late season and did our analysis on midseason data only. The limits on midseason data for the near-continuous flux tower data sets were defined as the first and last days of the growing season when midday NEE was greater than 5 μmol m^{-2} s^{-1}. Figure 1 shows the seasonal character of the NEE-PPFD relationship measured by the flux tower at sites 1a-1e in 1994. For the chamber data set from site 5 (Sallie's Fen) the midseason was defined as June through August. For all other
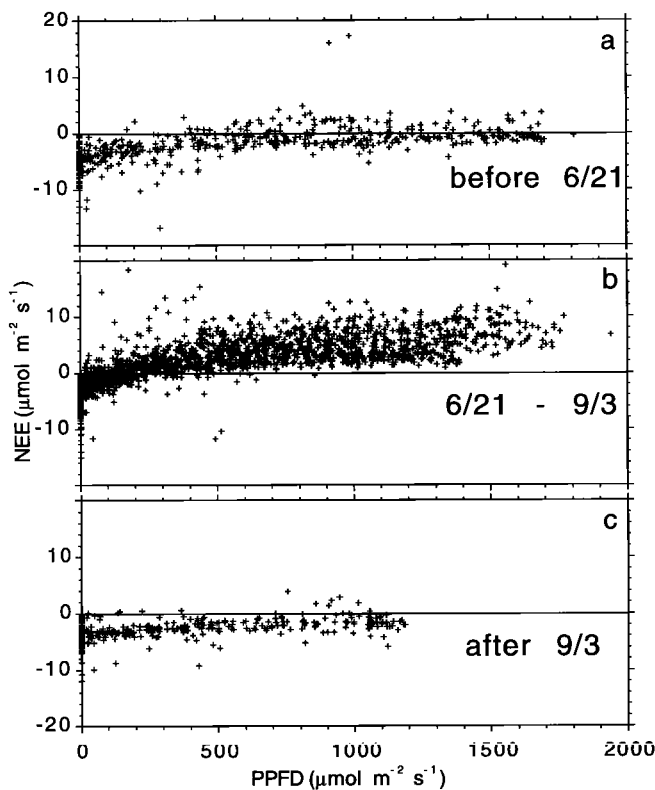

Figure 1. Seasonality in net ecosystem exchange-photosynthetic photon flux density (NEE-PPFD) relationship at the Boreal Ecosystem-Atmosphere Study (BOREAS) northern fen sites (Sites 1a-1e) as measured by the eddy-covariance flux tower [*Lafleur et al.*, 1997]. Data were divided into (a) early season (before June 21, 1994), (b) middle season (June 21, 1994 to September 3, 1994); and (c) late season (after September 3, 1994). In the early and late seasons, NEE was probably limited by ground and air temperatures and vegetational phenology. All analyses of NEE-PPFD relationships were done only on midseason data (see text for discussion).

chamber data sets, the midseason was bounded by the first and last days when an interpolated light response curve would show positive NEE for a PPFD of 500 μmol m^{-2} s^{-1}, and full light NEE was greater than 1.5 μmol m^{-2} s^{-1}. For all data sets, start of "midseason" ranged from late May to mid-June, and it ended in late August or early September. The exact dates varied because of differences in timing of thaw (even within a single peatland, e.g., Bubier et al., submitted manuscript, 1997) and fall senescence. These midseason delimiters were site-specific; they were not intended as an analysis of ecosystem phenological behavior, but simply as a means of isolating those data most suitable for developing a NEE-PPFD relationship comparable to upland ecosystem relationships reported in the literature [e.g., *Ruimy et al.*, 1995]. All remaining analyses in the study were done with midseason data only.

4.3.   Curve Fitting

Net ecosystem productivity equals gross productivity minus ecosystem respiration. Gross productivity will be a function of incident PAR. This functionality is often represented by a rectangular hyperbola [e.g., *Thornley and Johnson*, 1990], where there is a near-linear increase in productivity at low light levels and an asymptotic approach to a maximum productivity at high light levels. Plant maintenance respiration and heterotrophic respiration in the soil vary with air and soil temperature [*Amthor*, 1994], and should correspond to irradiance only indirectly through associated heating, with temperatures often lagging irradiance. Fitting a rectangular hyperbola to the NEE-PPFD relationship implicitly assumes that plant maintenance and heterotrophic respiration are uncorrelated with PPFD and that mean ecosystem respiration is equivalent to measured dark respiration. We used the general curve-fitting routine in Kalaidegraph (version 3.0, Abelbeck Software/Synergy Software, Reading Pennsylvania 19606) to fit the light response curves (NEE versus PPFD) with either a rectangular hyperbola

$$NEE = \frac{\alpha \, PPFD \, P_{max}}{\alpha \, PPFD + P_{max}} + R \tag{1}$$

or a straight line

$$NEE = \beta \, PPFD + R \tag{2}$$

where α is the initial slope of the rectangular hyperbola (also called the apparent quantum yield), P_{max} is the maximum gross productivity, R is the y axis intercept (or dark respiration value, $R<0$), and β is the slope of the linear fit. P_{max} plus R will be the asymptote for the NEE-PAR curve. These results can be compared directly with the results for other ecosystems reported by *Ruimy et al.* [1995]. Curve fits were done either to all midseason data from a single site or aggregated midseason data sets. *Ruimy et al.* [1995] define a "departure from linearity" as the difference between the correlation coefficients for a rectangular hyperbola fit and a linear fit to a particular data set; this was calculated for each data set. For additional comparison with the results of *Ruimy et al.* [1995], we calculate ecosystem productivity at full light, NEE$_{cup}$, using (1) at a PPFD equal to 1800 μmol m^{-2} s^{-1} (approximate full light on a sunny day in midsummer).

5. Results

5.1. Comparison by Measurement Method

We found little difference in the NEE-PPFD relationship between chamber and tower measurements at the BOREAS northern site (Figure 2 and Table 2). For the chamber data set from the rich fen (site 1e), the aggregated chamber data set (sites 1a-1e), and for the tower data set, the rectangular hyperbola generated a better fit (higher r^2), and the departure from linearity ranged from 0.08 (tower) to 0.11 (aggregated chamber data) (Table 2).

The timing of total ecosystem respiration and low-light productivity measurements was different for the two measurement methods. All tower "dark" measurements were at night; all chamber "dark" measurements were at midday with an opaque shroud in place for about 2-15 min. Rectangular hyperbola curve fits were made to aggregated fen tower data and chamber data (except Hudson Bay lowland fens, sites 7a and 7b; see discussion below). Midseason mean ecosystem
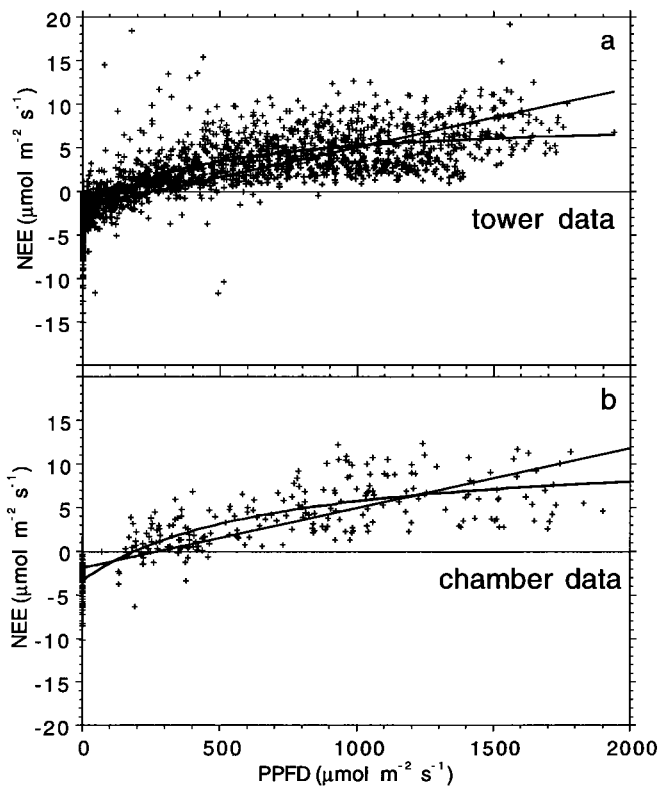

Figure 2. NEE-PPFD relationships at (a) the BOREAS northern fen peatland complex (Sites 1a-1e; Table 1) as measured in midseason 1994 by the eddy-covariance flux tower [*Lafleur et al.*, 1997], and (b) the BOREAS northern fen "tower fen" (Site 1e, Table 1) as measured by clear, static chambers in 1994 (Bellisario et al., submitted manuscript, 1997) and 1996 (Bubier et al., submitted manuscript, 1997). A rectangular hyperbola and a straight line were fit to each data set (see equations (1) and (2) in the text). Departures from linearity, defined as the r^2 for the rectangular hyperbola fit minus the r^2 of the linear fit, were 0.08 for the tower data and 0.09 for the chamber data. Note that for aggregated chamber data (sites 1a to 1e) the departure from linearity was 0.11 (see Table 2).

respiration rates (R) were nearly identical for the two methods: 2.73 (tower) and 2.76 (chamber) μmol m^{-2} s^{-1}. There were only a few very cloudy days when midday light was at around 200-300 μmol m^{-2} s^{-1}, so virtually all low-light measurements by the eddy-correlation towers were made either early or late in the day, while virtually all low-light chamber measurements were collected near midday with partially shrouded chambers. The towers observed a slightly higher initial slope to the NEE-PPFD curve ($\alpha_{tower} = 0.027$ versus $\alpha_{chamber} = 0.023$).

5.2. Site-by-Site Comparison

All five bog sites had low and comparable rates of mean ecosystem respiration (R) and peak ecosystem productivity (NEE$_{cap}$) (Table 2 and Figure 3a). The rich fen sites in Manitoba (site 1e) and Saskatchewan (site 2) had much higher values of NEE$_{cap}$ than the bogs (Table 2). The mean ecosystem respiration rate for site 1e, measured by chambers, was also much higher than the bog rates (all measured by chambers). The mean ecosystem respiration rate for site 2, measured by the tower, was lower than the chamber rich fen value; this is probably due, at least in part, to the numerous nighttime measurements in the tower data set, which would represent cooler temperatures on average. The rich fens in the Hudson Bay lowlands (sites 7a and 7b) had significantly lower rates for R and NEE$_{cap}$ than the other rich fen sites (Table 2 and Figure 3b). The Hudson Bay lowlands rich fens data were very similar to the bog class. Poor fens represent an intermediate peatland class, and their NEE-PPFD relationships were also intermediate (Table 2). The poor fen in the Experimental Lakes Area peatland (Site 6d) was very bog-like, while the other poor fens (sites 1c, 1d, and 5) were much more similar in behavior to the two BOREAS rich fens (Table 2). Though all the poor fens were *Sphagnum*-dominated, the poor fens at sites 1c, 1d, and 5 had much greater sedge biomass than the poor fen at site 6d.

5.3. Comparisons by Peatland Class

The NEE-PPFD data were aggregated into three peatland classes: bogs (all bog data), poor fens (all poor fen data), and rich fens (sites 1e and 2 only; Hudson Bay lowlands rich fen data excluded). All three aggregated data sets were fit with a rectangular hyperbola (Figure 4). The curve fit parameters (α, P_{max}, and R) were not significantly different for poor and rich fens, but all were significantly lower for bogs (Table 3). NEE$_{cap}$ was similar for poor and rich fens (6.5 and 6.9 μmol m^{-2} s^{-1}, respectively), and was almost 3 times lower for bogs (2.5 μmol m^{-2} s^{-1}) (Table 3). The mean ecosystem respiration (R) rate was also significantly lower for bogs than for poor and rich fens. Low pH and nutrient supply appear to retard respiration as well as photosynthesis in bog environments; more recalcitrant litter quality in bogs will also reduce respiration rates. The ability to fix CO_2 at low light was similar for all three peatland types, suggesting that they all utilize light similarly at very low PAR levels (α, Tables 2 and 3). A similar initial slope and lower asymptote indicates that bog productivity saturates at lower light levels than fen productivity.

The rich fen and poor fen data were combined into a single fen class, with and without the Hudson Bay lowlands rich fens; this data set included the BOREAS NSA tower (site 1), which sampled a mixture of peatland classes but is dominated by fens.

Table 2. Rectangular Hyperbola Curve Fit Parameters For Midseason Site Data Sets

Location, Site	Peatland	Method	n^a	α^b	$P_{max}{}^c$	R	$NEE_{cap}{}^c$	r^2	D^d
BOREAS NSA, 1a-1e	mixed	chamber	1394	0.024 (0.002)	10.5 (0.34)	-2.38 (0.01)	6.07	0.64	0.11
BOREAS NSA, 1a-1e	mixed	tower	2038	0.029 (0.002)	11.3 (0.31)	-2.93 (0.07)	6.36	0.68	0.08
BOREAS NSA, 1e	rich fen	chamber	313	0.023 (0.003)	15.1 (1.10)	-3.38 (0.25)	7.68	0.74	0.09
BOREAS SSA, 2	rich fen	tower	1352	0.025 (0.002)	11.5 (0.29)	-2.39 (0.10)	6.77	0.78	0.11
HBL, 7b and 7c	rich fen	chamber	701	0.010 (0.001)	4.0 (0.15)	-1.66 (0.07)	1.64	0.68	0.15
BOREAS NSA, 1c and 1d	poor fen	chamber	694	0.025 (0.003)	10.0 (0.48)	-1.98 (0.15)	6.79	0.70	0.12
ELA, 6d	poor fen	chamber	140	0.027 (0.006)	5.8 (0.38)	-2.43 (0.24)	2.74	0.67	0.23
New Hampshire, 5	poor fen	chamber	172	0.018 (0.002)	19.8 (1.30)	-5.18 (0.25)	7.11	0.89	0.08
HBL, 7a	bog	chamber	643	0.016 (0.002)	6.1 (0.25)	-2.27 (0.11)	2.73	0.64	0.12
Sweden, 4a-4c	bog	chamber	141	0.007 (0.002)	5.1 (0.64)	-1.06 (0.20)	2.56	0.60	0.05
BOREAS NSA, 1a and 1b	bog	chamber	387	0.019 (0.003)	7.1 (0.47)	-2.20 (0.17)	3.69	0.62	0.14
Frontenac, 3a-3c	bog	chamber	1262	0.017 (0.001)	4.1 (0.09)	-1.73 (0.05)	1.91	0.74	0.18
ELA, 6a-6c	bog	chamber	356	0.038 (0.008)	4.4 (0.26)	-2.51 (0.19)	1.62	0.47	0.24

Standard error given in parentheses. Abbreviations are as follows: NSA, northern study area; SSA, southern study area, HBL, Hudson Bay lowlands; and ELA, Experimental Lakes Area.
[a] Number of data points used in NEE-PPFD curve fits.
[b] Values given in μmol CO_2 μmol^{-1} PAR.
[c] Values given in μmol m^{-2} s^{-1}; NEE_{cap} calculated with equation (1) and PPFD = 1800 μmol m^{-2} s^{-1}.
[d] Departure from linearity is r^2 for rectangular hyperbolic fit minus r^2 for linear fit.

The NEE-PPFD relationship for fens was intermediate to the relationships for poor and rich fens (Table 3), except for ecosystem respiration, which was elevated by inclusion of the site 1 tower data (Table 2). Inclusion of Hudson Bay lowlands rich fens made the fen relationship more bog-like (Table 3).

5.4. Aggregated Data Set and Comparison to Other Ecosystems

As an ecotype, northern peatlands are distinctly different from the forest, grassland, and cropland classes presented in the review of Ruimy et al. [1995]. As a single aggregated data set, northern peatlands had both significantly lower productivity at high PPFD levels and lower apparent quantum yield at low light than cropland and forest ecosystems and the aggregated upland data set (grassland plus forest plus cropland) (Figure 5 and Table 3). NEE_{cap} was 4-5 times lower for peatlands (4.9 μmol m^{-2} s^{-1}) than for forests (20.2 μmol m^{-2} s^{-1}), grasslands (23.8 μmol m^{-2} s^{-1}), croplands (28.1 μmol m^{-2} s^{-1}), or aggregated uplands (23.8 μmol m^{-2} s^{-1}). The capacity to fix CO_2 at low light is also lowest in peatlands (0.020), 20-64% lower than for upland ecosystems. Respiration rates in peatlands were also lower (-2.44 μmol m^{-2} s^{-1}) than for upland systems (-3.46 to -5.39 μmol m^{-2} s^{-1}). The departure from linearity (D) for the aggregated peatland data (0.09) was similar to values reported by Ruimy et al. [1995] for forests (0.08) and cropland (0.10) and was much greater than the value for grasslands (0.02) (Table 3).

6. Discussion and Conclusions

The carbon flux values from these seven peatlands are consistent with other studies. Silvola et al. [1996a] measured soil respiration CO_2 fluxes with opaque, static chambers on bogs and fens in southern Finland. They observed respiration

rates of -0.5 to -5.0 μmol m^{-2} s^{-1} at 12°C, with higher rates at sites with more abundant understory vegetation. They attributed 35-45% of the total soil respiration to live roots [Silvola et al. 1996b]. Alm et al. [1997] operated clear, static chambers to measure NEE at a boreal, oligotrophic pine fen in Finland. They observed dark respiration rates of about -1.4 to -5.5 μmol m^{-2} s^{-1} and full light NEE rates of about 1.4 to 7.0 μmol m^{-2} s^{-1} Carex lawns generally had higher uptake rates than drier hummocks. Clymo and Hayward [1982] reported a maximum photosynthetic rate of 1.1 to 2.3 μmol m^{-2} s^{-1} for Sphagnum capillifolium.

In comparing NEE-PPFD relationships for tower and chamber data, two anticipated differences were not found. First, the departure from linearity for tower and chamber data were very similar (Table 2). Both Denmead [1991] and Ruimy et al. [1995] concluded that the NEE-PPFD relationship will be more linear when measurements are made with a micrometeorological tower than with chamber enclosures. They hypothesize three reasons for this: (1) the tower samples a larger and more varied landscape which could lead to a more linear response; (2) more diffuse radiation is likely to reach the green vegetation when the chamber method is used, which should enhance productivity at low light (this should lead to a higher initial slope, or α, in the PPFD-NEE curve); and (3) chambers often allow more light to reach the sides of the canopy, so more leaves reach PPFD saturation at lower light. Because of the very low stature of peatland vegetation, it is unlikely that the chamber had much influence on the radiation loading on the vegetation. However, the data indicate that the tower sampled the broader, more varied landscape, which probably accounts for its somewhat smaller departure from linearity. The chamber site 1e (rich fen) represents the landscape in the immediate vicinity of the tower, while the other chamber sites (poor fen, sites 1c and 1d; and bog, sites 1a and 1b) all represent components of the landscape within
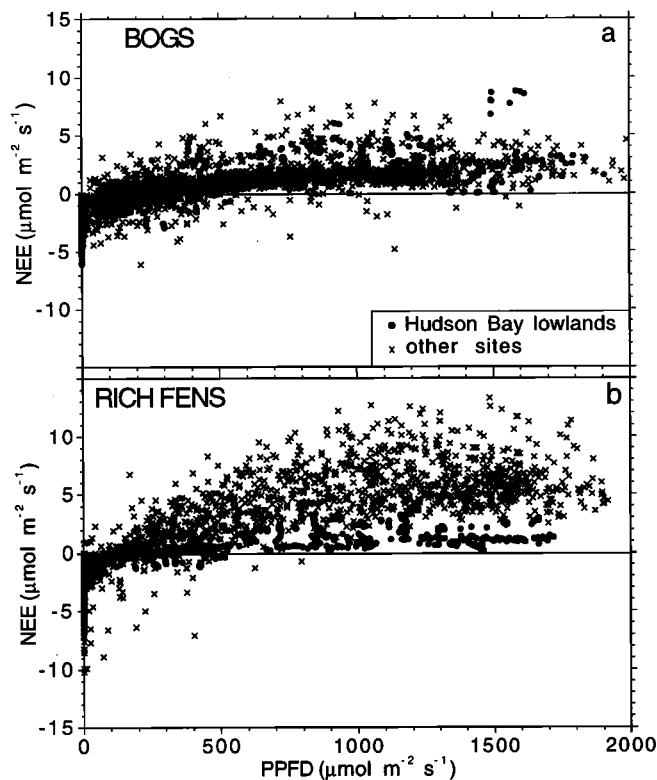
Figure 3. NEE-PPFD relationships for (a) all bog sites and (b) all rich fen sites. The solid circles represent data from the Hudson Bay lowlands, Kinosheo Bog in Figure 3a and the coastal and interior fens in Figure 3b. The crosses represent all other bogs (sites 1a-1b, 3a-3c, 4a-4c, and 6a-6c) in Figure 3a and the BOREAS southern study area fen (site 2) and the northern study area fen (site 1e) in Figure 3b. The NEE-PPFD relationship for the Hudson Bay lowlands rich fens is significantly different from the other rich fens (and very "bog-like"), while the NEE-PPFD relationship for the Hudson Bay lowlands bog is very similar to the other bogs.

the tower footprint. Tower curve fit parameters and NEE_{cap} fall between values for the rich fen (site 1e) and values for the aggregated chamber data set (Table 2). The tower data probably represents some average of the five chamber data sets, each weighted by the fractional area it occupies in the time-varying tower sample footprint.

Second, there was little apparent difference between mean seasonal ecosystem respiration for aggregated fen data sets as measured by the towers (all "dark" measurements made at night) and the chambers (all "dark" measurements made near midday) (Table 3). We anticipated differences due to temperature (cooler at night at 10 cm in soil if the water table was below 10 cm) which would lead to higher respiration rates for the chamber measurements, and also to "acclimatization" differences. The chamber dark measurements were made on vegetation that had been photosynthesizing in full light and was shrouded in darkness for only a few minutes before the measurements were made, while the tower dark measurements were made on plants that were under "natural" dark conditions during the night. This comparison could not be made for bogs as no tower data were collected.
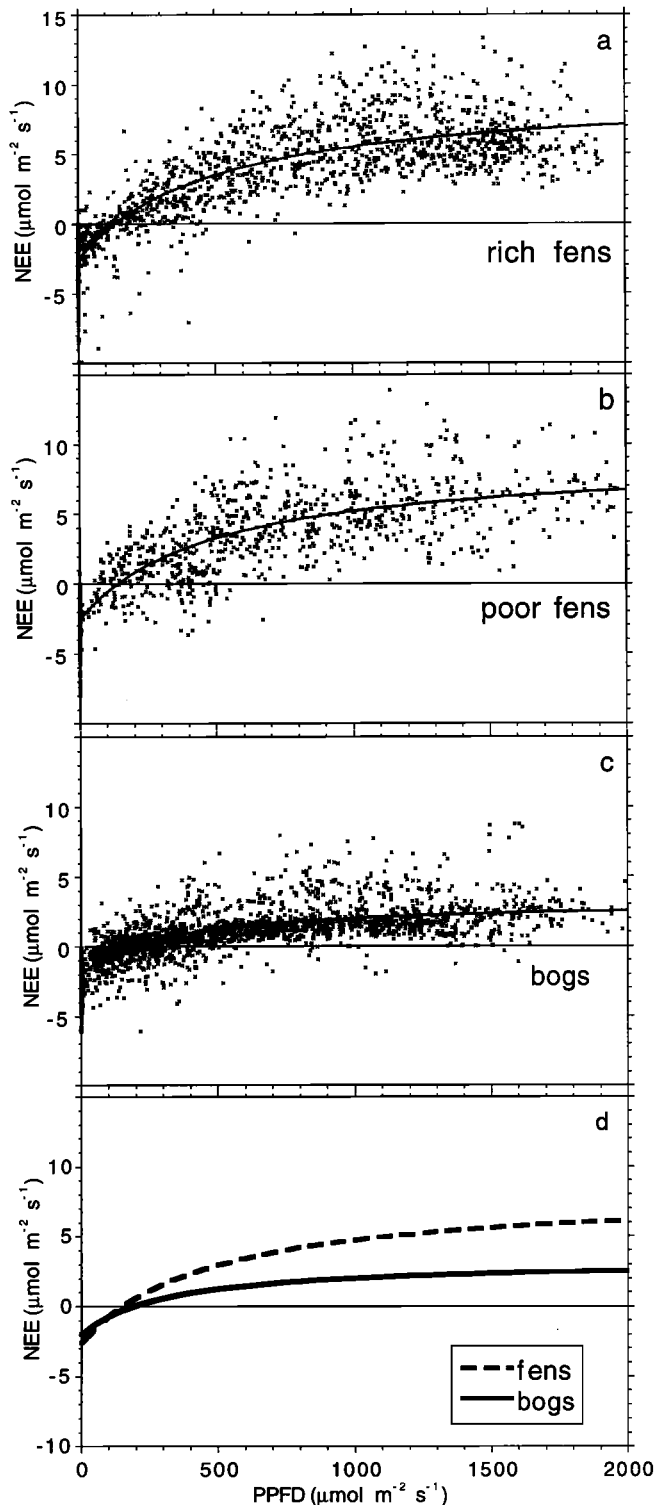
Figure 4. NEE-PPFD relationships for (a) rich fens (without the Hudson Bay lowlands' rich fen sites, see Figure 3), (b) all poor fen sites, and (c) all bog sites. Rectangular hyperbolic curves were fit to each site (parameters and goodness of fit data in Table 3). Rich fens and poor fens had very similar NEE-PPFD relationships, while bogs had significantly lower NEE at high light levels. (d) Rectangular hyperbola curve fits (equation (1)) to aggregated NEE-PPFD data sets for all bogs and all fens (Table 3).

Table 3. NEE-PPFD Curve Fit Parameters for Midseason Aggregrated Data Sets

Ecosystem	n^a	α^b	$P_{max}{}^c$	R	$NEE_{cap}{}^c$	r^2	D^d
Rich fens[e]	1665	0.024 (0.001)	12.1 (0.30)	-2.56 (0.09)	6.9	0.77	0.13
Poor fens	1043	0.024 (0.002)	11.5 (0.40)	-2.57 (0.13)	6.5	0.69	0.13
Bogs	2789	0.017 (0.001)	5.2 (0.11)	-1.99 (0.05)	2.5	0.61	0.14
Fens (tower)	3390	0.027 (0.001)	11.5 (0.20)	-2.73 (0.07)	6.6	0.72	0.10
Fens (chamber)[f]	1319	0.023 (0.002)	12.4 (0.40)	-2.76 (0.12)	6.8	0.70	0.12
Fens[g]	4709	0.026 (0.001)	11.8 (0.19)	-2.73 (0.06)	6.2	0.72	0.10
All fens	5410	0.023 (0.001)	10.8 (0.19)	-2.63 (0.06)	5.9	0.65	0.09
All peatlands	8199	0.020 (0.001)	9.2 (0.14)	-2.44 (0.05)	4.9	0.59	0.09
Forest[h]	718	0.040	35.3	-3.46	20.2	0.57	0.08
Grassland[h]	348	0.025	82.9	-5.39	23.8	0.80	0.02
Cropland[h]	560	0.056	46.9	-3.94	28.1	0.66	0.10
All uplands[h]	1362	0.044	43.4	-4.29	23.8	0.57	0.06

Standard error given in parentheses.

[a] n number of data points for NEE-PPFD curve fit.

[b] Values given in $\mu mol\ CO_2\ \mu mol^{-1}\ PAR$.

[c] Values given in $\mu mol\ m^{-2}\ s^{-1}$; NEE_{cap} calculated with equation (1) and $PPFD = 1800\ \mu mol\ m^{-2}\ s^{-1}$.

[d] Departure from linearity is r^2 for rectangular hyperbolic fit minus r^2 for linear fit.

[e] Includes tower data from BOREAS SSA fen (site 2) and chamber data from BOREAS NSA rich fen (site 1e).

[f] Includes chamber data from all poor fens and BOREAS NSA rich fen.

[g] Includes all tower data and chamber data from all poor and rich fens, except sites 7a and 7b..

[h] From *Ruimy et al.* [1995].

Our data show that fens are distinctly different from bogs in their NEE-PPFD relationship, but there was variability within the fen class. Rich fens in the Hudson Bay lowlands were more "bog-like" in their productivity than rich fens elsewhere. The data from the rich fens in the Hudson Bay lowlands suggests that something besides "traditional" peatland class indicators (e.g., pH, cations, and vegetation types) is needed to distinguish these low-productivity fens from other, higher-productivity fens. Although the highest photosynthetic and respiration rates were observed at the warmest fen site (site 5 in New Hampshire), mean summer (June, July, and August) air
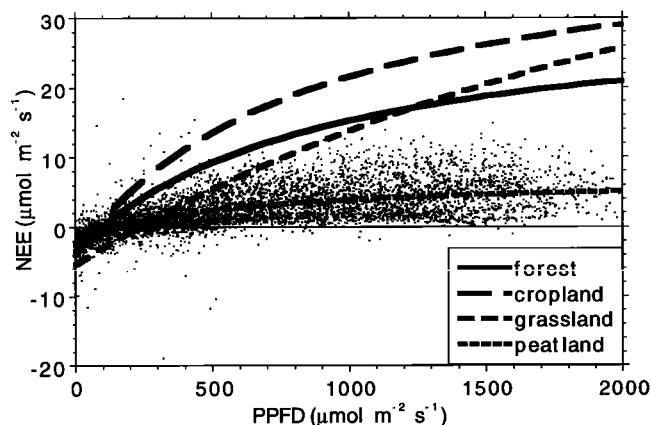

Figure 5. NEE-PPFD relationships for all northern peatland sites (this study) and for three major upland ecosystems [*Ruimy et al.*, 1995]. The lines represent rectangular hyperbolic curves fit to the four data sets (see Table 3 for parameters and goodness of fit data). Only northern peatland data points are shown. Northern peatlands have significantly lower productivity levels at moderate to high light than the upland ecosystems and lower ecosystem dark respiration rates.

temperatures do not appear to be very useful in explaining differences in the NEE-PPFD relationship among sites (Tables 1 and 2). For example, the mean summer air temperature at Moosonee, Ontario (13.8°C [*Mortsch*, 1994]) is very similar to that at Thompson, Manitoba (13.9°C [*Environment Canada*, 1993]), but the respiration rate at the rich fen near Thompson is twice that of the rich fen near Moosonee, and NEE_{cap} is 4.8 times larger (Table 2).

The low NEE rates observed at full light in the Hudson Bay lowland sites are consistent with other characteristics of the peatlands there. Plant productivity in the Hudson Bay lowlands is lower than in fens elsewhere. Ranges in ANPP for the Hudson Bay lowlands peatlands are 35-90 g m^{-2} [*Innanen*, 1991], compared with 200-400 g m^{-2} in rich fens elsewhere in Canada [*Szumigalski and Bayley*, 1996; Bubier et al., submitted manuscript, 1997]. Although herbs comprised more of the biomass in the fens than in the bogs in the Hudson Bay lowlands [*Whiting*, 1994; *Klinger et al.*, 1994], herb productivity may be much lower in the Hudson Bay lowlands fens than in other fens included in this study. Live and dead herb biomass ranged from 40 to 140 g m^{-2} in the Hudson Bay lowlands coastal and interior fens [*Whiting*, 1994], compared with 100-300 g m^{-2} in rich fens elsewhere [*Szumigalski and Bayley*, 1996; *Bellisario*, 1996; J. L. Bubier, unpublished data 1996].

In addition, seasonal average methane fluxes from Hudson Bay lowlands were unexpectedly low; sites with highest methane fluxes (open graminoid fens, bogs, and pools) had values ranging from 8 to 160 mg CH$_4$ m^{-2} d^{-1} [*Roulet et al.*, 1994]. By comparison, at the BOREAS northern study area peatland, seasonal average methane fluxes from open graminoid fens, bogs, and pools ranged from 92 to 380 mg CH$_4$ m^{-2} d^{-1} [*Bubier et al.*, 1995]; for the BOREAS southern study area fen, the seasonal average methane flux was about 200-300 mg CH$_4$ m^{-2} d^{-1} [*Suyker et al.*, 1996]. This positive relationship of site productivity and methane emission is

consistent with findings across a wide latitudinal gradient of wetland types [*Whiting and Chanton*, 1993]. The fact that the NEE-PPFD relationship for the bog at Hudson Bay lowlands was similar to other bogs and that the rich fens at Hudson Bay lowlands were similar to all bogs suggests that overall nutrient availability in the Hudson Bay lowlands may be sufficient to support productivity only at a level typical for bogs.

Despite the geographical and ecological ranges of the sites, the NEE-PPFD relationship is generally consistent across the northern peatlands represented in these data sets. There is a clear distinction between bogs and fens in the aggregated data sets and in most of the individual data sets. In classifying peatlands from a carbon flux perspective, distinguishing between bogs and fens would be more important than distinguishing poor fens from rich fens. In many studies, a number of fen classes are used for distinguishing the range of minerotrophic peatlands in North America [e.g., *Vitt et al.*, 1995]. *Gorham and Janssens* [1992] found that classifying peatlands into *Sphagnum*-dominated and brown moss-dominated types was a more useful and simpler division in terms of surface water acidity than maintaining several fen classes. However, our data show that in terms of NEE-PPFD relationships *Sphagnum*-dominated fens are more similar to brown moss-dominated fens than to *Sphagnum*-dominated bogs. Plant biomass (especially herbaceous plant biomass), which is determined by factors other than pH, for example, nutrient availability [*Malmer*, 1993; *Aerts and Caluwe*, 1994], may be a more relevant criteria than surface water acidity alone for distinguishing peatland productivity classes. *Szumigalski and Bayley* [1996] showed that shrub productivity decreased from bog to rich fen in a number of North American peatlands, but herb production increased. Bellisario et al. (submitted manuscript, 1997) found that *Carex* aboveground biomass was a good predictor of site productivity in the BOREAS NSA peatlands.

The data presented indicate that for global analyses northern peatlands should be considered as one distinct ecological class (or two classes). Peatland ecosystem respiration is about 30-50% lower than any of the upland classesreported by *Ruimy et al.* [1995] (Table 3). Maximum productivity (P_{max}) and full light productivity (NEE$_{cap}$) for bogs are only about 10% of the values for upland ecosystems, while fen values are about 25% of upland values (Table 3). However, most global carbon models do not include separate calculations for northern peatlands. The Frankfurt Biosphere Model [*Lüdeke et al.*, 1995] does make separate calculations; however, this model may have the wrong response for "mossy bogs" relative to other ecosystems. The function relating NPP to PPFD in the Frankfurt Biosphere Model has the initial slope of the curve increasing for decreasing leaf area index and decreasing productivity. However, this study has found that the initial slope of the NEE-PPFD curve α for the aggregated northern peatland data set is lower than the value for grasslands and is much lower than the values for croplands and forests; peak ecosystem productivity (NEE$_{cap}$) for peatlands is also much lower than the values for the three upland ecosystems (Table 3) [*Ruimy et al.*, 1995]. To accurately represent peatland landscapes in regional and global-scale ecosystem and climate models, it will be essential to develop appropriate algorithms and parameterizations describing

Table 4. Peatland Vegetation Tissue Decomposition Rates

Peatland	Tissue Type	k^a
Subarctic fens	sedges	-0.15 to -0.32
	ericaceous leaves and stems	-0.12
	Sphagnum	-0.06 to -0.09
Boreal bogs	sedges	-0.20 to -0.28
	ericaceous leaves and stems	-0.06 to -0.31
	conifer needles	-0.11 to -0.28
	Sphagnum	-0.04 to -0.58

Based on mass loss over 4 to 6 years (T.R. Moore, unpublished data, 1997).

[a] Parameter in fit of exponential mass loss equation, ln(mass remaining) = $c + kt$, with t in years.

peatlands (either as bogs and fens or as a single class) as a unique component of the land surface.

The relatively low capacity of peatlands to fix CO_2, compared to forests and grasslands, contrasts with their large storage of soil C and high soil C accumulation rates. There are a number of reasons for this retention of C in peatland soils. One is the infrequent occurrence of disturbances, particularly fire, in peatlands, whereas upland forest soils lose C during fires [e.g., *Trumbore and Harden*, 1997]. A second is the generally slow rate at which many peatland plant tissues decompose, compared to litter in upland forests [*Johnson and Damman*, 1993; *Verhoeven and Toth*, 1995]. Exponential decay constants (k) from tissues decomposing in subarctic fens and boreal bogs range from -0.05 year^{-1} for slowly-decomposing *Sphagnum* (especially the hummock-forming *Sphagnum fuscum*) to -0.3 year^{-1} for ericaceous plants and sedges (Table 4). In contrast, plant litter in upland temperate and boreal forests has k values frequently in the range of -0.1 to -0.2 year^{-1} for conifer needles to -0.3 to -0.5 year^{-1} for hardwood leaves [e.g., *Aber et al.*, 1990; *Moore*, 1984; *Taylor et al.*, 1991]. Third, the presence of a high water table in peatlands creates anaerobic conditions which slows the rate at which peat decomposes. Short- and long-term laboratory incubations of peat samples reveal that the ratio of aerobic:anaerobic CO_2 production averages 2.5 to 2.8 [*Moore and Dalva*, 1997; *Updegraff et al.*, 1995]. Laboratory peat columns in which the water table can be adjusted show that CO_2 emission rates when the water table is at depth of 40 to 50 cm are 4 to 6 times as large as when the water table is at the peat surface [*Moore and Dalva*, 1993; *Moore and Knowles*, 1989]. Finally, the waterlogged nature of peat soils and the presence of an insulating moss surface often keep the summer temperatures cool (4° to 10°C) at depths of 0.5 to 1 m, further slowing the rate of peat decomposition.

In conclusion, we are convinced that northern peatlands, because of their ubiquitous nature and large carbon stores, are an important component of the global carbon cycle. Whether aggregated into a single group or separated into bog and fen classes, the NEE-PPFD relationships for northern peatlands are significantly different than those for the upland systems. Within peatland types, differences in phenology and productivity obscure any finer classification. These NEE-PPFD relationships can be used to parameterize productivity

functions for bog and fen landscape classes in global carbon cycle models. There is a need to develop landscape classification algorithms for high-resolution remote sensing instruments so that the spatial distribution of northern peatlands can be determined.

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