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B. E. Law
328 Richardson Hall, College of Forestry, Oregon State University, Corvallis, OR 97331-5752, USA

E. Falge
Pflanzenökologie, Universität Bayreuth, 95440 Bayreuth, Germany

L. Gu
ESPM, University of California, Berkeley, CA 94704, USA

D. D. Baldocchi
ESPM, University of California, Berkeley, CA 94704, USA

P. Bakwin
NOAA/OAR, Climate Monitoring and Diagnostics Laboratory, 325 Broadway, Boulder, CO 80303, USA

See next page for additional authors

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Authors
B. E. Law, E. Falge, L. Gu, D. D. Baldocchi, P. Bakwin, P. Berbigier, K. Davis, A. J. Dolman, M. Falk, J. D. Fuentes, A. Goldstein, A. Granier, A. Grelle, D. Hollinger, I. A. Janssens, P. Jarvis, N. O. Jensen, G. Katul, K. Mahli, G. Matteucci, T. Meyers, R. Monson, W. Munger, W. Oechel, R. Olson, K. Pilegaard, K. T. Paw U, H. Thorgeirsson, R. Valentini, Shashi Verma, T. Vesala, K. Wilson, and S. Wofsy

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ELSEVIER

Agricultural and Forest Meteorology 113 (2002) 97–120

AGRICULTURAL AND FOREST METEOROLOGY

www.elsevier.com/locate/agrformet

Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation

B.E. Law[a,*], E. Falge[b], L. Gu[c], D.D. Baldocchi[c], P. Bakwin[d], P. Berbigier[e], K. Davis[f], A.J. Dolman[g], M. Falk[h], J.D. Fuentes[i], A. Goldstein[c], A. Granier[j], A. Grelle[k], D. Hollinger[l], I.A. Janssens[m], P. Jarvis[n], N.O. Jensen[o], G. Katul[p], Y. Mahli[q], G. Matteucci[r], T. Meyers[s], R. Monson[t], W. Munger[u], W. Oechel[v], R. Olson[w], K. Pilegaard[x], K.T. Paw U[h], H. Thorgeirsson[y], R. Valentini[r], S. Verma[z], T. Vesala[a1], K. Wilson[s], S. Wofsy[u]

[a] *328 Richardson Hall, College of Forestry, Oregon State University, Corvallis, OR 97331-5752, USA*
[b] *Pflanzenökologie, Universität Bayreuth, 95440 Bayreuth, Germany*
[c] *ESPM, University of California, Berkeley, CA 94704, USA*
[d] *NOAA/OAR, Climate Monitoring and Diagnostics Laboratory, 325 Broadway, Boulder, CO 80303, USA*
[e] *INRA Centre de Bordeaux, Unite de Bioclimatologie, BP 81, 33833 Villenave d'ornon Cedex, France*
[f] *Department of Soil, Water, and Climate, University of Minnesota, St. Paul, MN 55108, USA*
[g] *Alterra, P.O. Box 47, 6700 AA Wageningen, The Netherlands*
[h] *Atmospheric Science Group, LAWR, UC Davis, 122 Hoagland Hall, Davis, CA 95616, USA*
[i] *Department of Environmental Science, University of Virginia, Charlottesville, VA, USA*
[j] *Centre de Recherces de Nancy, Unite Ecophysiologie Forestieres, Equipe Bioclimatologie, 54280 Champenoux, France*
[k] *Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden*
[l] *USDA Forest Service, 271 Mast Road, Durham, NH 03824, USA*
[m] *Department of Biology, University of Antwerpen, Wilrijk, Belgium*
[n] *Institute of Ecology and Resource Management, University of Edinburgh, Darwin Building, King's Buildings, Edinburgh EH9 3JU, UK*
[o] *Risoe National Laboratory, DK-4000 Roskilde, Denmark*
[p] *School of the Environment, Duke University, Box 90328, Durham, NC 27708-0328, USA*
[q] *Institute of Ecology and Resource Management, University of Edinburgh, Darwin Building, King's Buildings, Mayfield Road, Edinburgh EH9 3JU, UK*
[r] *Department of Forest Environment and Resources, University of Tuscia, I-01100 Viterbo, Italy*
[s] *NOAA/ARL Atmospheric Turbulence and Diffusion Division, 456 South Illinois Avenue, Oak Ridge, TN 37831-2456, USA*
[t] *Department of Environmental, Population, and Organismic Biology, University of Colorado, Campus Box 334, Boulder, CO 80309, USA*
[u] *Department of Earth and Planetary Sciences, Harvard University, 20 Oxford Street, Cambridge, MA 02138, USA*
[v] *Department of Biology, San Diego State University, San Diego, CA, USA*
[w] *Environmental Science Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA*
[x] *Plant Biology and Biogeochemistry Department, Risoe National Laboratory, P.O. Box 49, DK-4000 Roskilde, Denmark*
[y] *Department of Environmental Research, Agricultural Research Institute, IS-112 Reykjavik, Iceland*
[z] *Department of Agricultural Meteorology, University of Nebraska-Lincoln, 244 L.W. Chase Hall, P.O. Box 830728, Lincoln, NE 68583, USA*
[a1] *Department of Physics, University of Helsinki, P.O. Box 9, FIN-00014 Helsinki, Finland*

Accepted 3 April 2002

* Corresponding author. Tel.: +1-541-737-6111; fax: +1-541-737-1393.
E-mail address: lawb@fsl.orst.edu (B.E. Law).

0168-1923/02/$ – see front matter © 2002 Elsevier Science B.V. All rights reserved.
PII: S0168-1923(02)00104-1

Abstract

The objective of this research was to compare seasonal and annual estimates of CO_2 and water vapor exchange across sites in forests, grasslands, crops, and tundra that are part of an international network called FLUXNET, and to investigating the responses of vegetation to environmental variables. FLUXNETs goals are to understand the mechanisms controlling the exchanges of CO_2, water vapor and energy across a spectrum of time and space scales, and to provide information for modeling of carbon and water cycling across regions and the globe. At a subset of sites, net carbon uptake (net ecosystem exchange, the net of photosynthesis and respiration) was greater under diffuse than under direct radiation conditions, perhaps because of a more efficient distribution of non-saturating light conditions for photosynthesis, lower vapor pressure deficit limitation to photosynthesis, and lower respiration associated with reduced temperature. The slope of the relation between monthly gross ecosystem production and evapotranspiration was similar between biomes, except for tundra vegetation, showing a strong linkage between carbon gain and water loss integrated over the year (slopes = 3.4 g CO_2/kg H_2O for grasslands, 3.2 for deciduous broadleaf forests, 3.1 for crops, 2.4 for evergreen conifers, and 1.5 for tundra vegetation). The ratio of annual ecosystem respiration to gross photosynthesis averaged 0.83, with lower values for grasslands, presumably because of less investment in respiring plant tissue compared with forests. Ecosystem respiration was weakly correlated with mean annual temperature across biomes, in spite of within site sensitivity over shorter temporal scales. Mean annual temperature and site water balance explained much of the variation in gross photosynthesis. Water availability limits leaf area index over the long-term, and inter-annual climate variability can limit carbon uptake below the potential of the leaf area present.
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Keywords: Gross ecosystem production; Ecosystem respiration; Net ecosystem exchange; Carbon balance; Eddy covariance

1. Introduction

The response of vegetation to the environment is a key global change issue that scientists are investigating by means of measurements and models on short- and long-time scales. Previous comparisons of the responses of terrestrial ecosystems of the world to the environment included measurements of aboveground production in relation to temperature, precipitation, and empirical estimates of evapotranspiration (ET). For example, earlier work suggested that annual productivity increased with mean annual temperature and precipitation (Lieth, 1972a,b; O'Neill and DeAngelis, 1981). Concurrently, leaf-level studies suggested a mechanism for optimal stomatal variation that regulates the relationship between water loss through transpiration and carbon uptake through assimilation in response to the environment (Cowan, 1977; Farquhar and Sharkey, 1982). More recently, modeling and measurements of mass and energy exchange at the canopy scale in boreal forests showed that cool air temperatures after soil thaw were conducive to rapid carbon uptake, but respiration increased above 17 °C, indicating that years with early springs and cool wet summers were associated with stronger annual net carbon uptake rates (e.g. BOREAS; Sellers et al., 1997a). Inter-comparisons of model results have also been conducted to investigate variation in simulations. Comparisons have been made on simulated sensible and latent heat fluxes amongst land-surface sub-models of general circulation models (Pitman and Henderson-Sellers, 1998; Pitman et al., 1999; Sellers et al., 1997b), and simulated net ecosystem production amongst dynamic global vegetation models (Cramer et al., 2001). With technological advancements and the establishment of an international network, FLUXNET (Baldocchi et al., 2001; Valentini et al., 2000; http://www.eosdis.ornl.gov/FLUXNET), we now have available a large body of data on terrestrial ecosystem exchange of mass and energy that is integrated at the stand level, with accompanying meteorological and biological measurements. This information can be used in combination with models to better understand temporal and spatial variation in fluxes.

The net ecosystem exchange (NEE) of CO_2 between the biosphere and the atmosphere is the balance between fluxes associated with photosynthetic assimilation by the foliage (gross ecosystem production (GEP)) and respiratory effluxes from autotrophs (R_a) and heterotrophs (R_h). Differences in annual NEE between locations might be attributable to disturbance history, climate, nutrition, biome type, and physiological differences associated with age (Law et al., 2001a;

Schulze et al., 1999, 2000). Environmental conditions may influence photosynthetic uptake and autotrophic and heterotrophic respiration differently. Research in European forests showed that there was no correlation between GEP and latitude, but annual ecosystem respiration increased with latitude, in spite of the decrease in mean annual temperature (Valentini et al., 2000). Other studies have shown that ecosystem respiration is primarily from soils (Janssens et al., 2001; Law et al., 1999a,b; Goulden et al., 1996b, 1998). Although strong correlations have been found between soil surface CO_2 efflux and temperature within sites, a poor correlation was found between decomposition of organic carbon in mineral soil and mean annual temperature across sites (e.g., Giardina and Ryan, 2000). Studies have also identified relations between periodicities or amplitudes in climate and plant processes, as well as temporal variation in responses of different ecosystem processes to environmental variables (Bowling et al., 2002; Woodward, 1987).

Although the measurement of ecosystem fluxes is useful for understanding responses to the environment at individual sites, we cannot measure ecosystem fluxes everywhere and continuously over the long-term. If our flux site information is to be used for spatial and temporal integration, we need to produce canopy scale response functions that the models can use and test.

Results from bottom-up biomass inventories, inverse modeling studies that combine flask measurements of carbon dioxide (CO_2) with global circulation models, and terrestrial modeling activities suggest that CO_2 fluxes strongly reflect the impacts of disturbance history, whereas inter-annual differences in carbon sources and sinks are likely to be driven primarily by the effect of climate on ecosystem processes (Schimel et al., 2000, 2002). Thus, a key issue for current and future research is to quantify the causal link between climate and CO_2 exchange for all major terrestrial ecosystems as a basis for model prediction.

The objective of this research was to compare seasonal and annual estimates of CO_2 and water vapor exchange across sites in forests, grasslands, crops and tundra, and to investigate the magnitude and variation in responses of vegetation to environmental variables, and the linkage between carbon uptake and water loss. The overall goal is to elucidate general responses within and between biomes and to provide information for modeling of carbon and water cycling across regions and around the globe. The intent is to provide insight into general response functions for modeling carbon and water processes for both regional and global climate models and identify the differences to show where land-surface models can be improved. This data set includes sites where temperature and precipitation co-vary seasonally (e.g. they increase together during summer months), and sites where they are decoupled (e.g. regions where drought occurs during the summer growing season), which allows us to determine if relations between processes and environmental variables are consistent for the pooled data.

2. Methods

This study represents a synthesis of data from flux sites in deciduous and evergreen forests, grasslands, crops, and tundra vegetation. The geographic range of the sites varies in latitude from 2° to 65°N and in longitude from 20°W to 25°E. The climatic zones include temperate continental, oceanic, Mediterranean, and boreal. Automated micrometeorological measurements were made of CO_2 and water vapor exchange over vegetation at the sites, and ancillary data, such as soil properties, leaf area index (LAI), and net primary productivity (NPP) were collected. The experimental sites are monotypic biomes representative of regional vegetation. Table 1 shows the characteristics and codes for the sites.

We limited this study to a subset of sites where climate and flux data have been analyzed, following consistent methods, and archived (Falge et al., 2001; Baldocchi et al., 2001; Aubinet et al., 2000). Carbon, water vapor, and energy fluxes were estimated with the eddy covariance technique from towers above the vegetation canopies. Flux systems comprised three-axis sonic anemometers that measured wind speed and virtual temperature, infrared gas analyzers that measured concentrations of water vapor and CO_2, and a suite of software for real-time and post-processing analysis. Fluxes were averaged half-hourly, and the records in the database were evaluated for data quality.

Although the intent is to obtain continuous NEE measurements, missing data occur because of system failure or data rejection. The average data coverage over the year was 65–75%. For our study, we filled

Table 1
Site characteristics, including growing season temperature (T_{grow}), annual precipitation (P), water balance ($\sum(ET - P)$), LAI, net ecosystem CO_2 exchange (NEE), and ecosystem respiration (R_e) (missing values indicate there were not enough data through the year after data screening, see Section 2)

Site (symbol)	Location	Elevation (m)	Climate[a]	T_{grow} (°C)	P (mm)	$\sum(ET - P)$	Age[b]	LAI[c] ($m^2\,m^{-2}$)	NEE ($g\,C\,m^{-2}$ per year)	R_e ($g\,C\,m^{-2}$ per year)	Period	Citation
Evergreen coniferous forests												
Aberfeldy, Scotland (AB)	56°37′N, 3°48′W	340	O	8.9	958	−991	14	8	−707	1384	1997	Valentini et al. (2000)
				9.0	1242	−887			−487	1270	1998	
Blodgett Forest, CA, USA (BL)	38°54′N, 120°38′W	1315	M		2210		10 (CC, P 1980)	3.2 (1997)			1997	Law et al. (2001c), Xu et al. (2001)
								4.5 (1998)				
Bordeaux, France (BO)	44°05″N, 0°05′E	60	O	17	995	−313	30 (CC, P 1970)	2.8	−525	1638	1997	Hassika and Berbigier (1998)
Duke, NC, USA (DU)	36°2′N, 79°8′W	163	T	17.2	748	−243	17 (CC, B, P 1983)	5.2	−538	941	1998	This study
				17.0					−651	843	1999	
Flakaliden, Sweden (FL)	64°07′N, 19°27′E	225	B	12.6	198	100	31	2	−173	526	1997	Lindroth et al. (1998)
				10.2	429	−206			53	798	1998	
Howland, ME, USA (HL)	45°12′N, 68°44′W	60	TC	11.9	1045	−692	90	5.5	−246		1996	Hollinger et al. (1999)
				13.8	710	−350			−256		1997	
Hyytiälä, Finland (HY)	61°51′N, 24°17′E	170	B	13.3	540	−223	35 (1997)	3	−228	720	1997	Markkanen et al. (2001), Vesala et al. (1998)
				11.5	681	−455			−264	700	1998	
Saskatchewan, Canada (JP)	53°55′N, 104°41′W	580	B	15.8	403		75–90	2			1994	Baldocchi et al. (1997)
Loobos, Netherlands (LO)	52°10′N, 5°45′E	25	T	13.3	758	−339	80		−323	1114	1997	Valentini et al. (2000)
				13.2	1266	−901			−199	1154	1998	
Metolius, OR, USA (ME)	44°30′N, 121°37′W	915	T	9.7	867	−239	45250	2.1	−287	885	1996	Law et al. (1999a,b), Law et al. (2000, 2001a)
				9.6	488	−74			−257	996	1997	
Manitoba, Canada (NB)	55°54′N, 98°30′W	259	B	12.4	375	−123	53–155	4.8	20	836	1995	Goulden et al. (1998)
				13.1	337	−104			−3	861	1996	
				13.5	372	−126			5	820	1997	
				13.3	300	90			−36	782	1998	
Norunda, Sweden (NO)	60°05′N, 17°28′E	45	TB	11.9	656	−311	100	5	−75		1996	Lindroth et al. (1998)
				10.0	483	−102			101		1997	
Niwot Ridge, CO, USA (NR)	40°02′N, 105°33′W	3050	TS	9.7	680		95	3.7–4.3[d]			1999	Monson et al. (2002)
Tharandt, Germany (TH)	50°58′N, 13°38′E	380	TC	12.0	1412	−914	140	6			1997	Valentini et al. (2000)
				11.5	990	−482					1998	
				12.6	951	−411					1999	
Weiden Brunnen, Germany (WE)	50°09′N, 11°52′E	780	SM	11.7	1304	−1071	40	5	24	1325	1998	Valentini et al. (2000)
Wind River, WA, USA (WR)	45°49′N, 121°57′W	355	O	9.5	2528		400–500	11	−446		1999	Chen et al. (2002)
Mixed evergreen and deciduous forests												
Braschaat, Belgium (BR)	51°18′N, 4°31′E	10	TC	17.5	662		67	3	76	1033	1997	Janssens et al. (2001)
				17.0	1042	−676			105	1218	1998	
Park Falls, WI, USA (WL)	45°56′N, 90°16′W	470–500	TC	17.1	1092	−714	60–80	4	−34	865	1997	Berger et al. (2001); K. Davis, pers. commun.
				15.1	525	−118			55	1081	1998	
				18.1	706	−312			44	829	1999	
Deciduous broadleaf forests												
Gunnarsholt, Iceland (GU)	63°50′N, 20°13′W	78	O	9.5	1168		5	1.4			1997	Valentini et al. (2000)
				10.9							1998	
Hesse, France (HE)	48°40′N, 7°05′E	300	TC	13.7	924	−589	30	6	−145	1009	1997	Valentini et al. (2000), Granier et al. (2000a)
				16.6	974	−633			63	1429	1998	
				16.3	1096	−687			−182	1296	1999	
Harvard Forest, MA, USA (HV)	42°32′N, 72°11′W	180–490	T	17.4	970	−554	90	5.5	−195	792	1992	Goulden et al. (1996a); this study

				16.6	1157	−656			−193	1003	1993	
				17.7	968	−527			−150	957	1994	
				18.4	938	−457			−242	875	1995	
				17.2	1379	−942			−148	937x	1996	
				16.0	908	−463			−234	942	1997	
				17.9	954	−524			−87	981	1998	
				19.0	1011	−516			−197	1043	1999	
Soroe, Denmark (SO)	55°29′N, 11°39′E	40	TO	15.5	527	−267	78	4.8	−55	1131	1997	Pilegaard et al. (2001)
				13.7	791	−525			−48	1347	1998	
				14.6	1705	−1455			−88	1237	1999	
Vielsalm, Belgium (VB)	50°18′N, 6°0′E	450	T	11.1	1261	−1012	60–90	4.5	−507		1998	Valentini et al. (2000)
Walker Branch, TN, USA (WB)	35°57′N, 84°17′W	365–380	T	19.6	1253	−716	58	6.0	−470	1038	1995	Wilson and Baldocchi (2000a), Wilson et al. (2000b), Wilson et al. (2001)
				21.2	1705	−1151			−576	1031	1996	
				20.2	1450	−839			−618	1037	1997	
				22.2	1663	−1103			−870	1052	1998	
Willow Creek, WI, USA (WC)	45°47′N, 90°3′W	480	TC	19.2	694	−103	35–70	4.2	−180	769	1999	B.D. Cook, pers. commun.
Evergreen broadleaf forests												
Castelporziano, Italy (CP)	41°45′N, 12°22′E	3	M	14.9			50	3.5	−518	1165	1997	Valentini et al. (2000)
				15.5	249				−653		1998	
Sky Oaks, CA, USA (Sky: young, Sko: old)	33°22′N, 116°37′W	1420	M	17.1			10 (Sky)	3 (Sko)		240 (Sky)	1999	This study
							78 (Sko)					
Grasslands												
Little Washita, OK, USA (LW)	34°58′N, 97°59′W		TC	21.6	938	−463			109		1997	Meyers (2001)
				23.3	715	−314			422	552	1998	
Shidler, OK, USA (SH)	36°51′N, 96°41′W		TC	23.2	1112	−504		0.0–2.9	−362	1354	1997	This study
Tundra												
Atqasuk, AK, USA (AT)	70°29′N, 157°25′W	1	TU								1999	Oechel et al. (2000)
Barrow, AK, USA (BA)	70°18′N, 156°38′W	1	TU		36 (June–August)		Mature tussock tundra, wet sedge	1.0–1.5			1998	Oechel et al. (2000)
							8000–10000				1999	
Happy Valley, AK, USA (HP)	69°08′N, 148°50′W	366	TU				8000–10000	1.0–1.5			1994	Oechel et al. (2000)
											1995	
Upad, AK, USA (UP)	70°16′N, 148°53′W	3	TU				8000–10000	1.0–1.5			1994	Oechel et al. (2000)
Crops												
Bondville, IL, USA (BV)	40°N, 88°18′W	213	TC	22.6	709	−168	C_4, C_3; annual rotation corn, soybeans	0–3.8	−543	894	1997	Meyers (2001)
				22.7	930	−283			133	713	1998	
				23.1	813	−193			−634	945	1999	
Ponca City, OK, USA (PO)	36°45′N, 97°05′W		TC	21.4	1184	−327	C_3 winter wheat	0–5	−155	1240	1997	This study

[a] B: boreal; M: Mediterranean; O: oceanic; SM: sub-oceanic, mountainous; *T*: temperate; TC: temperate, continental; TS: temperate, subalpine; TO: temperate, oceanic; TB: temperate/boreal transition; TU: tundra.
[b] CC: clearcut, B: burned, P: planted, with year planted.
[c] LAI is m^2 one-sided leaf area per m^2 ground.
[d] LAI is 3.7 if wind is from the east, and 4.3 if wind is from the west fetch.

date gaps by means of standardized methods (look-up table method, Falge et al., 2001) to provide complete data sets. Average NEE was compiled for a maximum of 6 (or 4) seasonal periods × 23Q_{PPFD}-classes × 35T_a-classes. Q_{PPFD}-classes (photosynthetic photon flux density (PPFD)) consisted of 100 μmol m^{-2} s^{-1} intervals, ranging from 0 to 2200 μmol m^{-2} s^{-1}, with a separate class for $Q_{PPFD} = 0$. Similarly, T_a-classes (air temperature) were defined as 2 °C intervals ranging from −19 to 49 °C. The procedure produced tables of NEE means and standard deviations for each class. Gaps in the look-up tables were interpolated linearly. To allow fast access to multiple records, the data are stored in a unified format, available in daily, weekly, monthly, and annual time resolution for a variety of potential uses.

Ecosystem respiration (R_e) was calculated for each half-hour from site-specific relationships between nocturnal NEE and soil temperature, and summed into weekly and monthly values. For further details on R_e calculations, see Falge et al. (2002). Briefly, R_e was derived from exponential regressions between nighttime fluxes at high friction velocity and soil temperature. An Arrhenius equation (Eq. (1)) from Lloyd and Taylor (1994) was used with a reference temperature (T_{ref}) of 283.16 K. $R_{e,T_{ref}}$ and E_a are the fitted parameters. $R_{e,T_{ref}}$ is the ecosystem respiration rate at T_{ref}; E_a is the activation energy in J mol^{-1}; R is the gas constant (8.134 J K^{-1} mol^{-1}); T_K is the soil temperature at 5 cm depth:

$$R_{e,night} = R_{e,T_{ref}}\, e^{(E_a/R((1/T_{ref})-(1/T_K)))} \quad (1)$$

A single value of E_a was calculated for each site over the entire year. The parameter $R_{e,T_{ref}}$ was evaluated for a 30-day moving window starting from January 1. The derived parameter sets were applied over the entire year and the half-hourly results were summed into daily values.

GEP represents the net rate of carboxylation and oxygenation by the enzyme ribulose bisphosphate carboxylase/oxygenase (RUBISCO), which constitutes about half of the soluble protein in leaves in C_3 plants, and can interact with CO_2, leading to photosynthesis (Nobel, 1991). GEP does not include photorespiration, so it is not equivalent to leaf chamber measurements of net assimilation. GEP was calculated from the difference between daytime NEE and daytime R_e, where a net gain of carbon by the ecosystem is negative in the convention of micrometeorological measurements and R_e is positive. We compared weekly, monthly, and annual estimates of NEE, GEP, and ET, and investigated responses to environmental variables. Data were removed from the analyses if more than 25% of the data for the year was missing, and more than 65% of the data for the month. Because we applied a consistent approach of data analysis and screening, annual estimates in Table 1 may differ slightly from previously published data for individual sites. Some vegetation types or sites do not appear in some analyses because of limited data (e.g., annual GEP and water balance for evergreen broadleaf and tundra vegetation).

Uncertainty estimates have been discussed in detail in Moncrieff et al. (1996) and in papers from individual sites (e.g., Anthoni et al., 1999; Goulden et al., 1996b; Grelle, 1997). Systematic errors include uncertainties in gas analyzer calibrations related to calibration gases (∼±3%) and changes in analyzer calibration because of residue on the analyzer optics (e.g., ∼±5–10%). Instabilities in calibration coefficients from diurnal changes in temperature and pressure are often assumed to be <5%. Uncertainties in wind speed and virtual temperature measured by the sonic anemometers are estimated to result in ∼±2% uncertainty in the scalar fluxes (Grelle, 1997). These systematic errors amount to ∼±12% of the daytime CO_2 fluxes (Anthoni et al., 1999). Systematic micrometeorological problems might be much more substantial for certain sites. These potential problems include missing low frequency fluxes, spectral degradation caused by closed-cell instruments, horizontal and vertical advection (Massman and Lee, 2002; Eugster and Siegrist, 2000), and lack of energy balance closure and uncertainty of its importance to CO_2 fluxes.

Janssens et al. (2001) suggested that total R_e (24 h) can be overestimated by as much as 15% if nocturnal data are used, because of daytime inhibition of leaf respiration (Brooks and Farquhar, 1985). Comparisons of nocturnal eddy covariance fluxes and scaled-up chamber estimates of R_e have indicated that underestimation due to advective losses might be as high as 30% of R_e at some sites on calm nights (Law et al., 1999a; Lavigne et al., 1997; Goulden et al., 1996b). This bias in this study was minimized because we used only flux data from periods of high friction velocity ($u*$). We used site-specific thresholds of $u*$, above which the parameters of an exponential regression between

nighttime NEE and soil temperature did not change anymore. At a few sites in complex terrain, or where low wind conditions prevailed at night, we calculated R_e and nocturnal NEE from alternative methods. We used scaled-up chamber estimates for nocturnal fluxes at ME (see Table 1; Law et al., 2000). For WB (see Table 1), we parameterized the CANOAK model with seasonal chamber measurements on soils, stems, and foliage and replaced nocturnal eddy covariance measurements with modeled nocturnal NEE (R_e), following model validation with daytime fluxes (Wilson et al., 2000b). We measured diffuse and direct incident PPFD at a subset of sites and used the data to evaluate the association between NEE and light quality.

The start and end dates of the growing season were identified by the week that was the first of two or more consecutive weeks with negative NEE (net carbon uptake; Falge et al., 2002). We used mean daily air temperature to calculate the mean growing season temperature for this period. We calculated site water balance from the difference between daily ET and daily precipitation (P_{daily}), summed weekly, monthly, and yearly:

$$\sum(\mathrm{ET}_{daily} - P_{daily}) \quad (2)$$

This is a reasonable estimate of water balance, which has been used in the past (e.g., Budyko, 1984). Runoff components were ignored in this application. Another method is to add soil water storage to precipitation (e.g., Running and Coughlan, 1988), but not all sites have continuous soil moisture measurements. Eq. (2) includes rain interception as evaporation (15–25% of rainfall, with greater interception in more dense canopies) and evaporation from soil surfaces, but it could underestimate the intensity of water stress.

3. Results and discussion

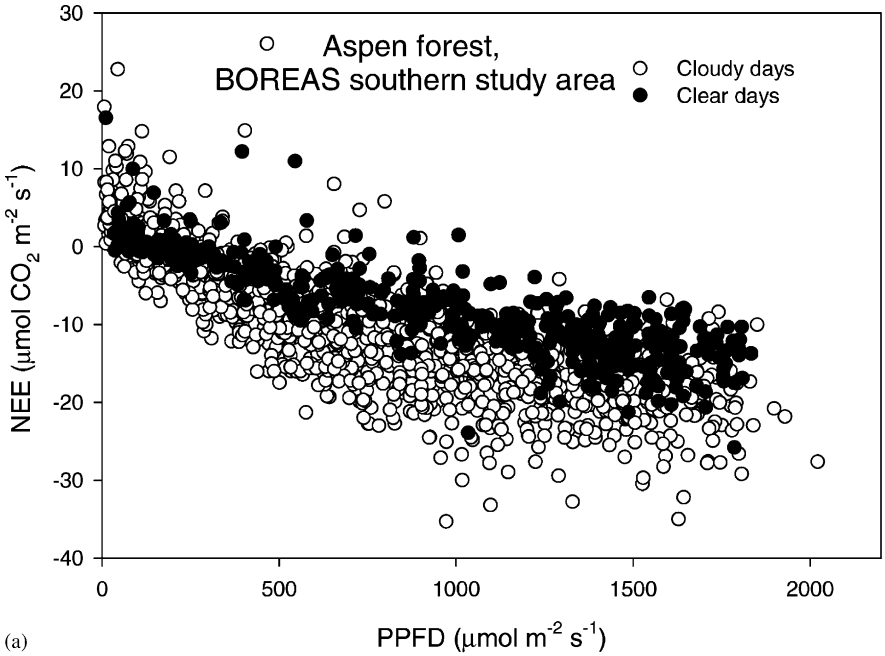
3.1. Light quality

For a subset of sites, we separated radiation data into clear and cloudy sky conditions using two criteria. First, a clearness index (the ratio of global solar irradiance at the surface to extraterrestrial solar irradiance) must increase smoothly with solar elevation angle. Second, the curve of the relation between the clearness index and solar elevation angle must form a boundary line. The remaining data were considered to be cloudy sky conditions.

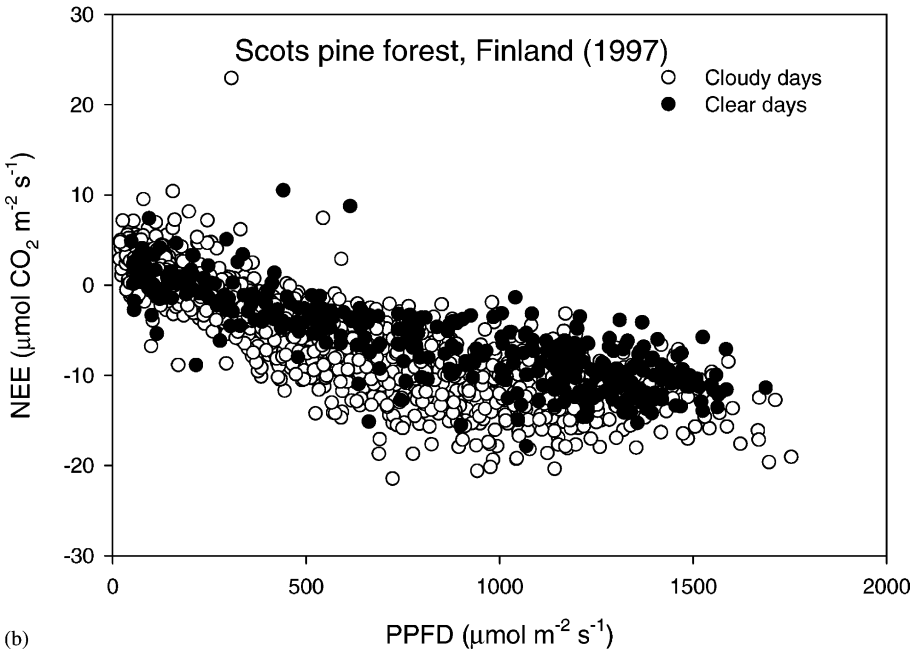
The highest solar irradiance for a given solar elevation angle occurs on partly cloudy days, not on clear days. This is due to a phenomenon termed ‘cumulus solar irradiance reflection’ by Segal and Davis, 1992 or ‘cloud gap effect’ described in Gu et al. (1999, 2001a). On cloudy days, sunlit ground surfaces are located at the end of solar beam paths through gaps formed by individual clouds in the vicinity. These areas receive the same amount of direct radiation as under clear sky conditions, but the incident diffuse radiation is increased due to light scattering and reflection from clouds in the vicinity (Oke, 1978). There can be as many bright cloudy periods as there are bright sunny periods during the growing season (e.g. when moisture is not limiting, and connective cumulus cloud formation dominates), as evident in a frequency analysis in a tropical forest (Gu et al., 2001b).

Cloud-cover results in a greater proportion of diffuse radiation and constitutes a higher fraction of light penetrating to lower depths of the canopy (Oechel and Lawrence, 1985). Goulden et al. (1997), Fitzjarrald et al. (1995), and Sakai et al. (1996) showed that net carbon uptake was consistently higher during cloudy periods in a boreal coniferous forest than during sunny periods with the same PPFD. Hollinger et al. (1994) found that daily net CO_2 uptake was greater on cloudy days, even though total PPFD was 21–45% lower on cloudy days than on clear days.

For a given solar elevation angle, decreases in total PPFD indicate changes in sky conditions from clear to cloudy, along with an increase in diffuse radiation, whereas air and soil temperature and vapor pressure deficit (VPD) tend to decrease (Gu et al., 1999). Ecosystem respiration decreases with air and soil temperatures, when water is not limiting, and leads to more net carbon uptake (more negative NEE) for a constant level of gross photosynthesis. For the same PPFD and temperature, respiration may be reduced under clear sky compared with cloudy conditions, perhaps because more soil moisture is available under cloudy conditions, and this may lead to higher soil respiration during early morning or late afternoon. Stomatal conductance (g_s) is a function of available water and evaporative demand, so that g_s tends to be higher at low VPDs, allowing more photosynthetic



(a)



(b)

Fig. 1. NEE of CO_2 in relation to diffuse and direct PPFD for (a) a boreal aspen forest, and (b) a boreal coniferous forest. Net carbon uptake was greater under diffuse sky conditions. (c) Gross photosynthesis in relation to PPFD for sunlit and shaded leaves, modeled with CANVEG.

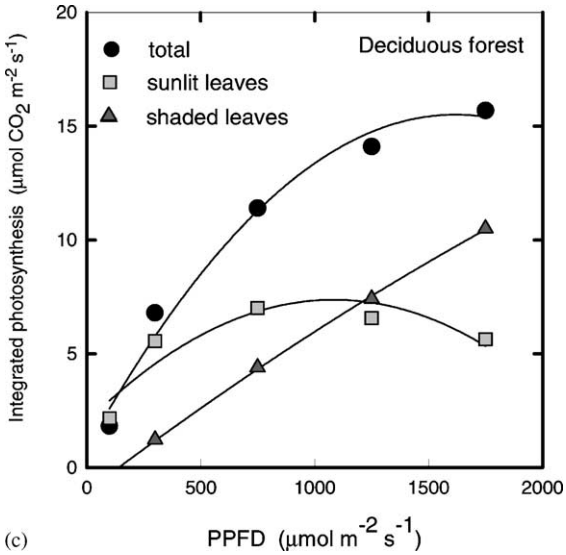


Fig. 1. (*Continued*).

carbon uptake. Therefore, when we plot NEE against total PPFD, based on solar elevation angles, we might not observe relationships similar to leaf response curves, which saturate at high levels of light.

Because photosynthetic efficiency is greater with diffuse radiation, it is important to evaluate NEE in relation to diffuse versus direct PPFD (Gu et al., 2001a). We found that NEE is more positive (less net carbon uptake) for clear sky than for cloudy conditions in boreal aspen and Scots pine forests (Fig. 1a and b). Simulations with the CANVEG model (Wilson et al., 2000b; Law et al., 2001b) demonstrate that photosynthesis is a linear function of PPFD for shade leaves and a curvilinear function of PPFD for sunlit leaves in a deciduous forest (Fig. 1c). Most process oriented models now distinguish sunlit and shade leaves; however, field data on diffuse and direct PPFD are sparse for model input (let alone total PPFD data) and often have to be modeled based on direct PPFD estimates and daily difference in minimum and maximum temperature (e.g., Thornton and Running, 1999).

3.2. Temperature

Respiration by soil autotrophs and heterotrophs can account for up to 75% of ecosystem respiration (Law et al., 2001a; Goulden et al., 1996b; Lavigne et al., 1997; Janssens et al., 2001). At individual sites, respiration is correlated with temperature in the short-term, when water availability is not limiting soil processes (Law et al., 2001d; Lavigne et al., 1997; Lloyd and Taylor, 1994). On a monthly basis, the relationships between R_e and T_{av} (Fig. 2a and b) were good, but this result is confounded by the use of half-hourly air temperature and nocturnal NEE to estimate R_e. The exponential coefficient for the relation between monthly R_e and T_{av} for the deciduous broadleaf forests ($R_e = 46.4\exp(0.056x)$, $r^2 = 0.61$) corresponds to a Q_{10} of 1.8, close to the value of 2 that is typically used as a default in modeling respiration. The relationship between R_e and T_{av} was generally better for deciduous broadleaf forests (Fig. 2b) than for evergreen coniferous forests (Fig. 2a), which appear to have better correlations within site. The slopes of the relationship for individual evergreen coniferous sites were smaller for sites that were subject to drought during the growing season (e.g., BL and ME in Fig. 2a; see Table 1). The R_e for the boreal NO (see Table 1) site in Fig. 2a (vertical lines) was much higher than the R_e for the other coniferous sites, a result of previous soil drainage, which provided a large amount of accumulated substrate for heterotrophic respiration (Valentini et al., 2000). This result stresses the importance of knowing site history and the influence of recent site disturbance on decomposition rates. Boreal forests in northern latitudes typically have soil that is wetter for longer periods (Grace and Rayment, 2000). Respiration rates can be higher than those of terrestrial ecosystems at lower latitudes that experience periods of soil water deficits.

Monthly NEE was poorly correlated with T_{av} and T_{grow}, but respiration and photosynthesis, which contribute to NEE, probably respond to temperature differently. The relative controls of temperature and light on photosynthesis vary seasonally with changes in leaf area and biochemistry, and photosynthesis is limited at temperature extremes. Heterotrophic respiration can be limited by substrate quality and quantity, in addition to temperature and moisture, and this can have a large effect on total ecosystem respiration.

Although R_e correlates with temperature at a given site under moist conditions, we found a poor correlation between annual R_e and mean annual temperature (T_{av}) across sites (linear and exponential temperature response $r^2 = 0.15$, 0.14, respectively). The relation was poorer when we used growing season temperature

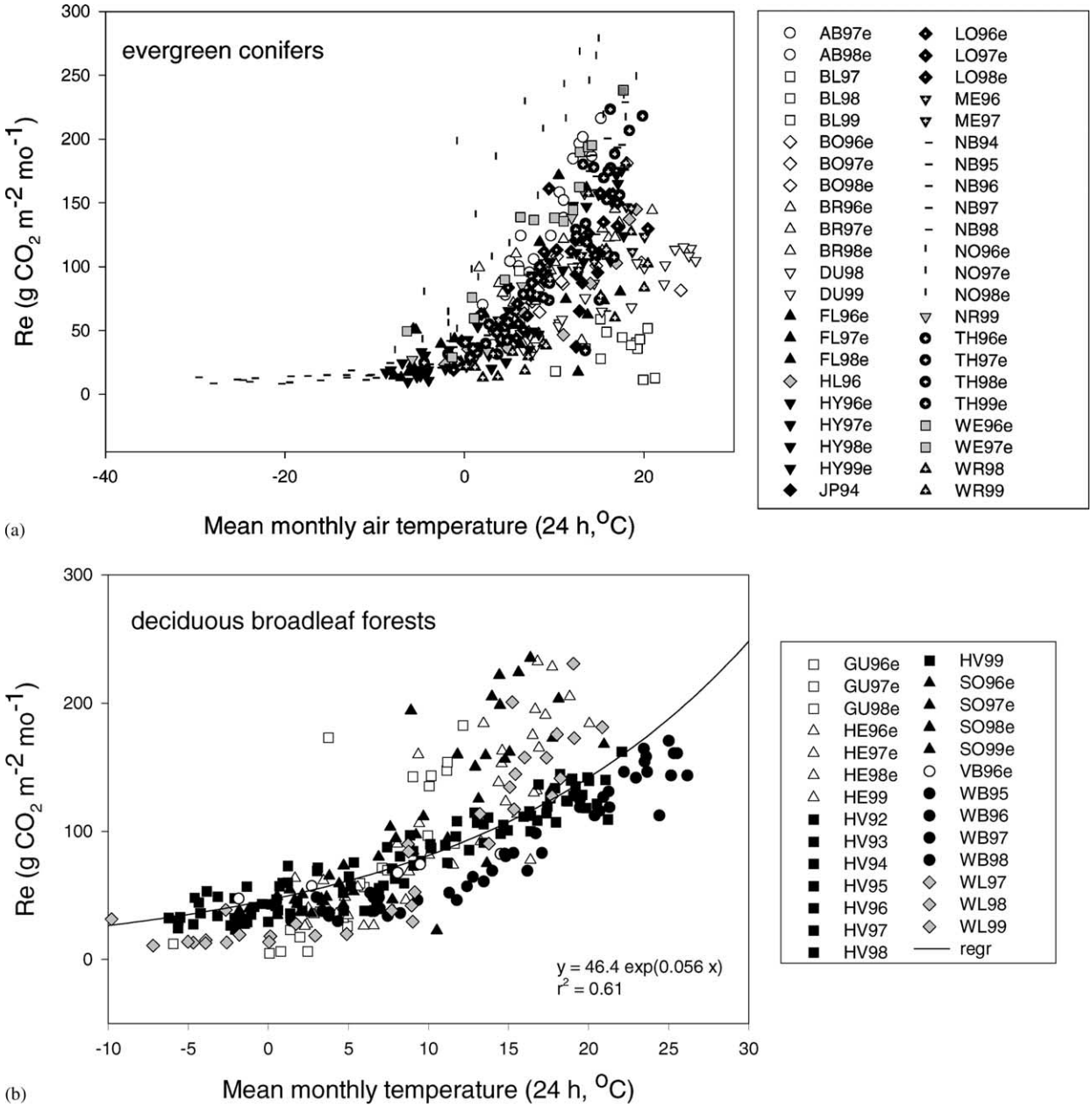


Fig. 2. Monthly cumulative ecosystem respiration increased with mean air temperature temperature at (a) evergreen coniferous forests and (b) deciduous broadleaf forests. Monthly GEP increased with temperature in evergreen coniferous forests.

(T_{grow}). Computations have suggested that annual estimates of respiration for gross carbon budgets can be improved by including daily and seasonal temperature amplitudes (Ryan, 1991). Yet, over long periods of time (e.g., years to decades) across sites, heterotrophic decomposition might be influenced more by substrate quality and quantity (Giardina and Ryan, 2000; Liski et al., 1999).

Table 2
Regression results for evergreen coniferous forests (EC), deciduous broadleaf forests (DB), grasslands (GR), crops (CR), and tundra (TU), where the equation is $y = a + bx$

Y variable	X variable	Intercept, a	Slope, b	r^2	SEE
Annual GEP (EC, DB, GR)	$\sum(\mathrm{ET} - P)$	955	−0.48	0.29	275
Annual GEP (all sites)	T_{av}	852	47	0.50	246
Annual GEP (EC, DB, GR)	$T_{av} \times \sum(\mathrm{ET} - P)$	943	−0.06	0.64	188
Annual GEP	LAI	838	92.2	0.12	291
LAI	$\sum(\mathrm{ET} - P)$	2.4	−0.004	0.39	1.1
Annual NEE (all sites)	$\sum(\mathrm{ET} - P)$	−70.8	0.24	0.12	225
Annual NEE (all sites)	T_{av}	−60.7	−21.5	0.17	240
Monthly GEP (all sites)	ET	11.2	2.8	0.58	67
Monthly GEP (EC)	ET	30.4	2.4	0.58	58
Monthly GEP (DB)	ET	−0.4	3.2	0.78	50
Monthly GEP (GR)	ET	−67.9	3.4	0.72	64
Monthly GEP (CR)	ET	−31.6	3.1	0.50	116
Monthly GEP (TU)	ET	0.6	1.5	0.44	30

Much of the dynamic response of processes to climate is lost in annual estimates, because of factors such as phenological influences. Annual NEE was poorly correlated with mean annual temperature ($r^2 = 0.17$; Table 2). However, mean annual air temperature explained 50% of the variation in GEP across sites (Fig. 3). We caution that there could be autocorrelation in that GEP was calculated from the difference between daytime NEE and daytime R_e, which was calculated from the relation between half-hourly nocturnal NEE and soil temperature. Valentini et al. (2000) showed that, for the EUROFLUX sites, annual

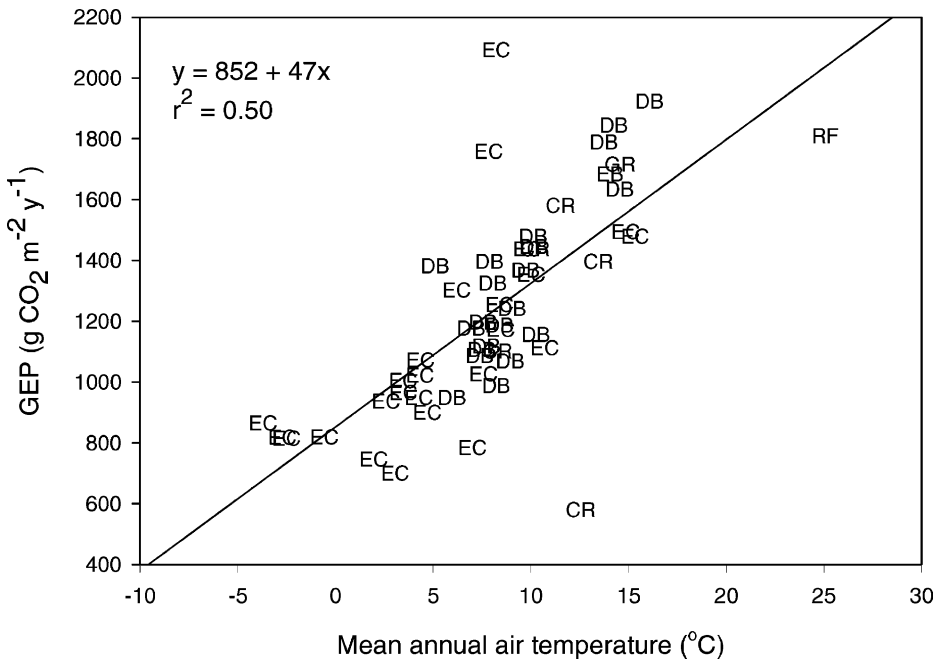


Fig. 3. Mean annual air temperature explained 50% of the variation in GEP across biomes. Symbols are for evergreen coniferous forests (EC), deciduous broadleaf forests (DB), evergreen broadleaf forests (EB), and grasslands (GR).

NEE decreased with latitude (40°–70°N), but there was no latitudinal trend in GEP. They suggested that ecosystem respiration was the main determinant of the relationship. In the EUROFLUX study, annual GEP ranged from ∼800 to 1600 g C m^{-2} per year for sites that were not intensively managed. For a broader range of sites, Fig. 3 shows that annual GEP varied from 700 g C m^{-2} per year in a boreal forest (FL site; see Table 1) to 1800 g C m^{-2} per year in a tropical forest (MA site; see Table 1). GEP is the integrated photosynthetic response to climate, nutrients, and disturbance and can vary considerably within a small latitudinal range. For example, at 44°N latitude in the United States (OTTER project), there exist mild maritime, montane, and cold, semi-arid conditions across a 350 km east-west swath. As a result, forest NPP was five times greater for conifers in the mild maritime climate than for the semi-arid ponderosa pine and juniper sites (Law and Waring, 1994). Likewise, simulated GEP varied eightfold from 300 g C m^{-2} per year at the semi-arid sites to 2400 g C m^{-2} per year at the milder sites (Williams et al., 1997). Thus, we would not expect to see a latitudinal trend in GEP, because of the climatic variation within latitude and the effects of disturbance or forest management on LAI and GEP.

The relation between annual NEE and GEP is shown in Fig. 4. The slope of the relation was 0.44 for evergreen conifers and 0.67 for deciduous broadleaf forests (intercepts 285 and 618 g C m^{-2} per year, respectively). The ratio R_e/GEP averaged 0.83 across all sites (range 0.55–1.2), with values >1 (i.e., net loss of CO_2) for boreal forests (NB; see Table 1) and

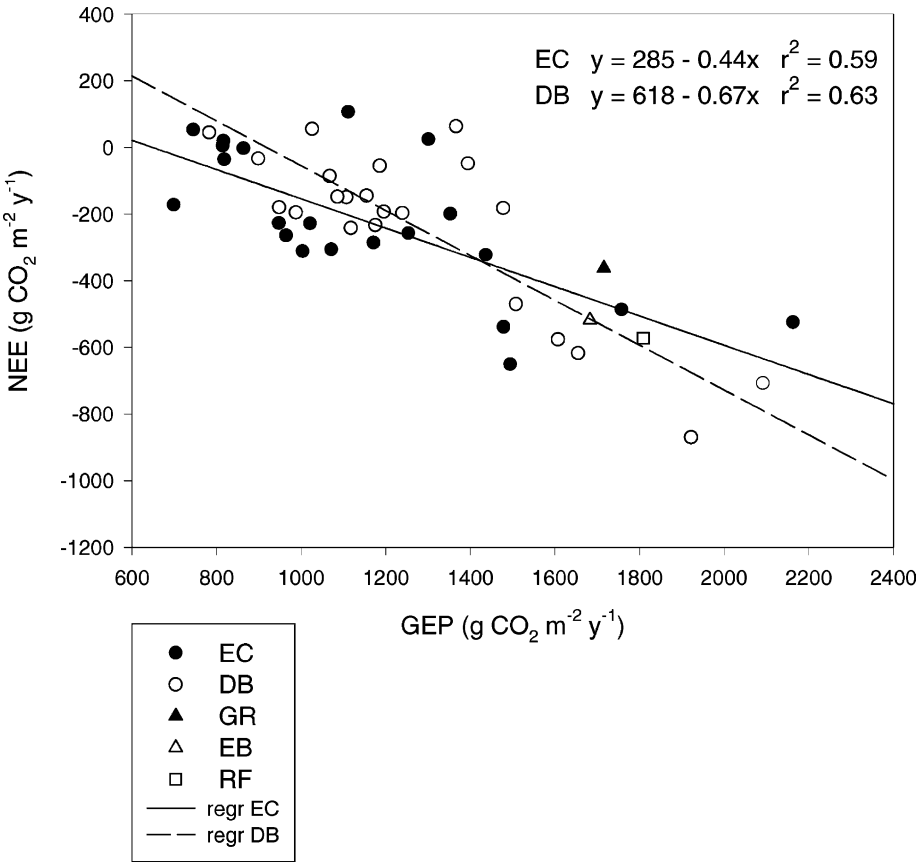


Fig. 4. The relation between annual NEP and GEP, where NEP = −NEE. The regressions are shown for evergreen coniferous forests (EC) and deciduous broadleaf forests (DB).

ecotonal temperate/boreal forests (WL and FL), as well as for northern temperate forests (BR, WE, and HE), and a cropland (BV). The ratio includes short- and long-term effects on processes. In 1998, the BV crop of soybeans had high decomposition rates of residual left from the previous corn crop (C_4) under no-till agricultural practices. Excluding the BV site, the common feature of the sites with a ratio >1 is that these sites are generally cooler, with an average mean annual temperature of 4.7 °C, compared with the overall mean of 8.4 °C. The R_e/GEP ratio was lowest for grasslands (mean 0.74 versus 0.82 for deciduous broadleaf forests and 0.85 for coniferous forests), presumably because of less investment in respiring plant tissue compared with forests. Because grasslands typically burn more frequently than other vegetation types, this ratio could be an underestimate of the loss of CO_2 to the atmosphere over a longer time frame. It would be useful for carbon management purposes to evaluate carbon use efficiency or NEE over the long-term (e.g., several decades) to include such disturbance effects on carbon fluxes and storage.

3.3. Water

Water stress is the most common limitation to growth of vegetation (Kozlowski et al., 1991). The annual water balance (Eq. (2)) of most sites was negative, indicating more precipitation entering the sites than the amount of water lost through evaporation and transpiration. Remaining water was runoff or infiltration into the soil where it might have percolated to the water table. A caveat is that the micrometeorological instruments can lead to underestimates of ET under wet conditions because water droplets may form on the sonic anemometers and open path sensors. In addition, the energy balance lacks closure at most sites (see Wilson et al., 2002), which can result from underestimation of the components, including ET. A positive water balance was observed only at Flakaliden, Sweden (FL) and Manitoba, Canada (NB), both of which are boreal coniferous forests (Table 1). The NB soils are clay, organic, and some sandy deposits, derived predominantly from glacial deposits; FL has saturated peaty soil. The boreal coniferous forest in Finland (HY; see Table 1) did not show a positive annual water balance, possibly because soil in Finland (HY) is haplic podzol and till dominated by fine sand, which drains freely, a common feature of Finnish soil.

The annual site water balance explains 29% of the variation in annual GEP amongst forests and grasslands (Fig. 5a; Table 2). Earlier studies combined temperature and water balance ($T \times P/\mathrm{PET}$, where T is the mean annual temperature, P the annual precipitation, and PET (potential evapotranspiration) $= 0.18 \times$ growing season length $\times T_{\mathrm{grow}}$) as an indicator of favorable growing conditions, and found a good correlation with the nutrient pool available to support photosynthesis (O'Neill and DeAngelis, 1981). We found a weak correlation between a similar index ($T_{\mathrm{grow}} \times \sum(\mathrm{ET} - P)$) and GEP ($r^2 = 0.33$) amongst forests and grasslands. Using mean annual air temperature in the index ($T_{\mathrm{av}} \times \sum(\mathrm{ET} - P)$) resulted in a good correlation with GEP ($r^2 = 0.64$; Fig. 5b). The potential leaf area for a site is a long-term response to site water balance. For the sites with LAI data ($n = 21$), we found that annual water balance explained about 39% of the variation in LAI (Fig. 5c). The maximum LAI has been shown to correlate well with site water balance across a strong climatic gradient (Gholz, 1982; Grier and Running, 1977). In addition, environmental limitations to gross photosynthesis and carbon allocation influence the long-term potential leaf area, so there is somewhat of a correlation between site water balance, LAI, and GEP. On an annual basis, however, we found a poor correlation between GEP and LAI. Short-term variation in light quality, water availability, and VPDs can reduce photosynthesis below the potential of the leaf area present. In conifers, even though elongation of new needles may be limited during a drought year, the reduction in leaf area might not become apparent until the following year. Leaf longevity also plays a role-sites with the shortest needle longevity (e.g. 2 years) were in milder climates and had relatively high GEP. Finally, some of the water transpired could be deep soil water stored from previous years that is within reach of tree roots, leading to less water stress than might be expected under current climate conditions (Williams et al., 2001; Jones, 1992).

NEE and R_e were weakly correlated with site water balance, and the temperature–water balance index ($T_{\mathrm{grow}} \times \sum(\mathrm{ET} - P)$; NEE $r^2 = 0.11$), suggesting that respiration is controlled more strongly by other factors. Nevertheless, much of the inter-annual variability

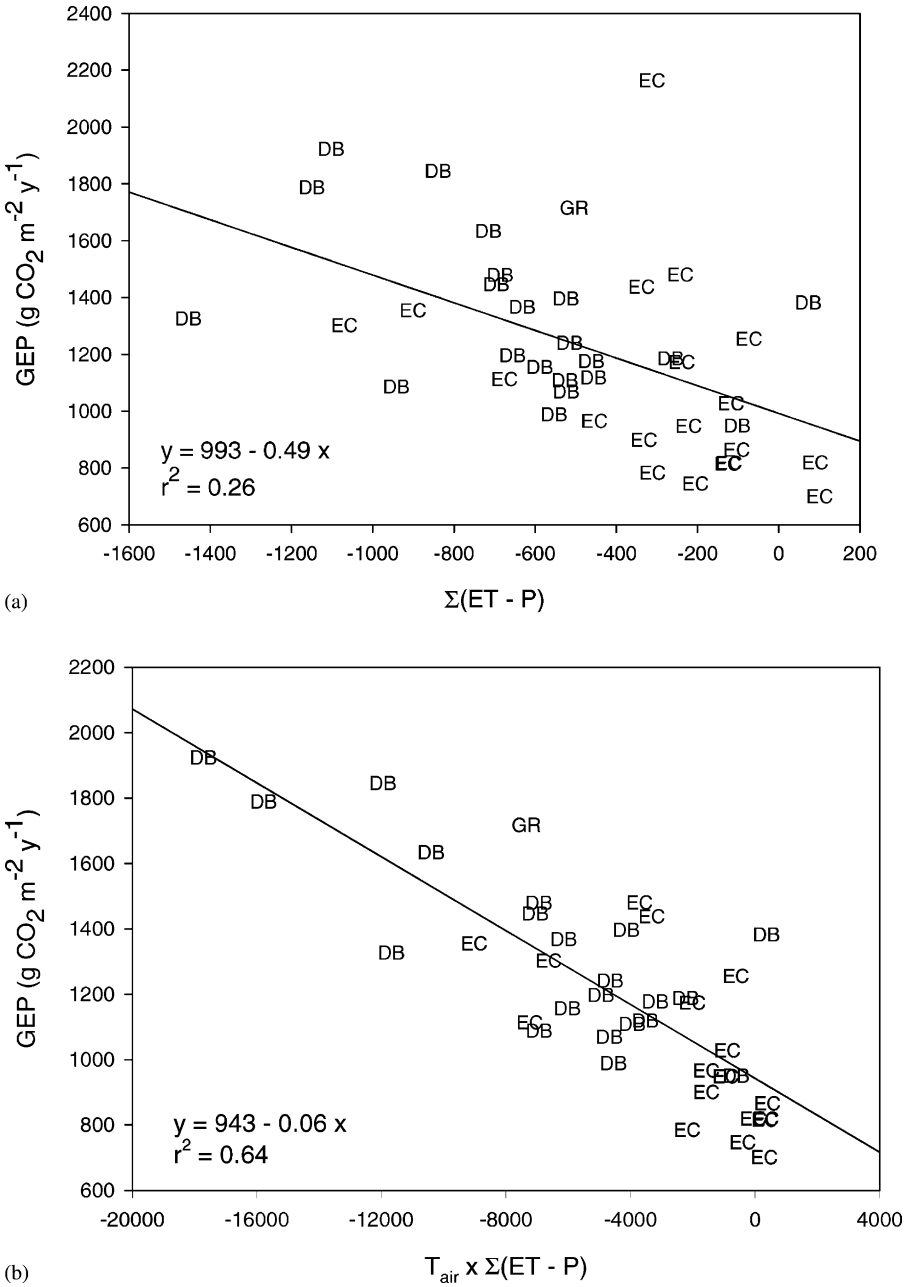
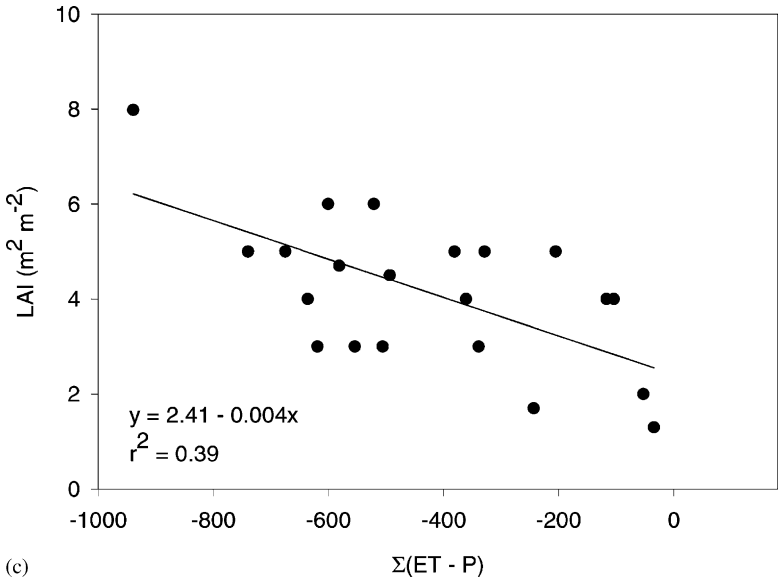


Fig. 5. (a) Annual site water balance, calculated from integrated ET minus precipitation ($\sum(\mathrm{ET} - P)$, explains 29% of the variation in GEP across biomes. (b) The product of mean annual temperature and site water balance explains 53% of the variation in annual GEP. (c) Annual site water balance explains 39% of the variation in LAI. Symbols are for evergreen coniferous forests (EC), deciduous broadleaf forests (DB), evergreen broadleaf forests (EB), and grasslands (GR).



(c)

Fig. 5. (*Continued*).

in NEE at some evergreen (ME; see Table 1) and deciduous forests (HE; see Table 1) has been attributed to drought (Granier et al., 2000b; Law et al., 2000) because of water limitations to carbon uptake during the growing season and increased respiration with temperature.

Monthly GEP increased with ET across sites, with a strong correlation for deciduous broadleaf forests and the weakest correlation for tundra vegetation (Fig. 6a–d). The slope of the relationship indicates the amount of carbon taken up in photosynthesis relative to the amount of water lost by the ecosystem through evaporation and transpiration, integrated over the year. It can be considered an indicator of ecosystem water use efficiency (WUE). The slopes were similar between vegetation types (Fig. 6e), except for tundra vegetation (slopes $= 3.4\,\mathrm{g\,CO_2/kg\,H_2O}$ for grasslands, 3.2 for deciduous broadleaf forests, 3.1 for crops, 2.4 for evergreen conifers, and 1.5 for tundra vegetation). Crops at the BV site (Fig. 6c; Table 1) are alternated annually between soybeans (C_3), and corn (C_4) and the slope for this site alone is 5.4 ($r^2 = 0.89$). GEP is derived from eddy flux R_e and NEE, and R_e at the BV site includes a large amount of heterotrophic respiration from decomposing crop residuals, as mentioned earlier. The slope of the relation between GEP and ET was very low for the BL ponderosa pine plantation (Fig. 6a; Table 1) during a summer of extreme drought when cavitation was thought to have occurred, limiting carbon uptake (Law et al., 2001c). Excluding the BL site, the slope was 3.0 for evergreen conifers ($r^2 = 0.73$). Within deciduous broadleaf forests, the amount of carbon uptake for a given amount of water vapor loss was greater for beech and poplar forests than for oak/maple forests, with the exception of WL (see Table 1), which includes conifers as well as poplars. Photosynthetic uptake was low in deciduous broadleaf forests, grasslands, crops, and tundra until ET exceeded 10–30 $\mathrm{kg\,H_2O\,mol^{-1}}$, probably because evaporation occurred before photosynthetically active leaf area was present.

Kelliher et al. (1990) suggested that maximum ET was similar between the forest ecosystems they reviewed despite a fivefold range of LAI. They attributed this finding to plasticity in the partitioning of ET between the canopy and the understorey/soil surface, noting that: (1) additional units of LAI above a value of about 5 do not enhance canopy transpiration; (2) understorey and soil evapotranspiration tend to be inversely proportional to LAI. Several studies support this postulate (Black and Kelliher, 1989; Law et al., 2001b; Lafleur et al., 1993; Baldocchi et al., 1997). Sapflow measurements scaled to stands demonstrated

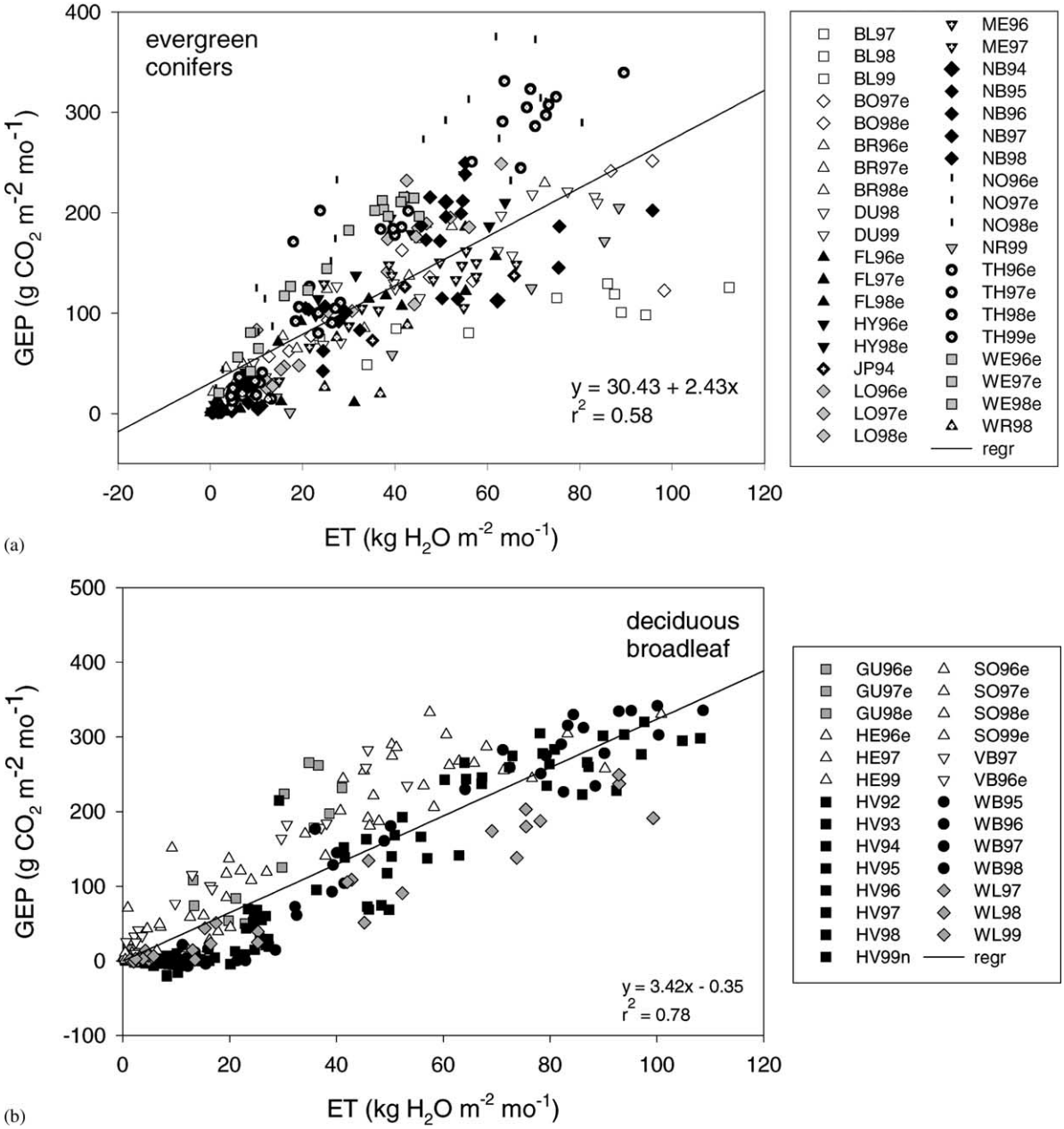
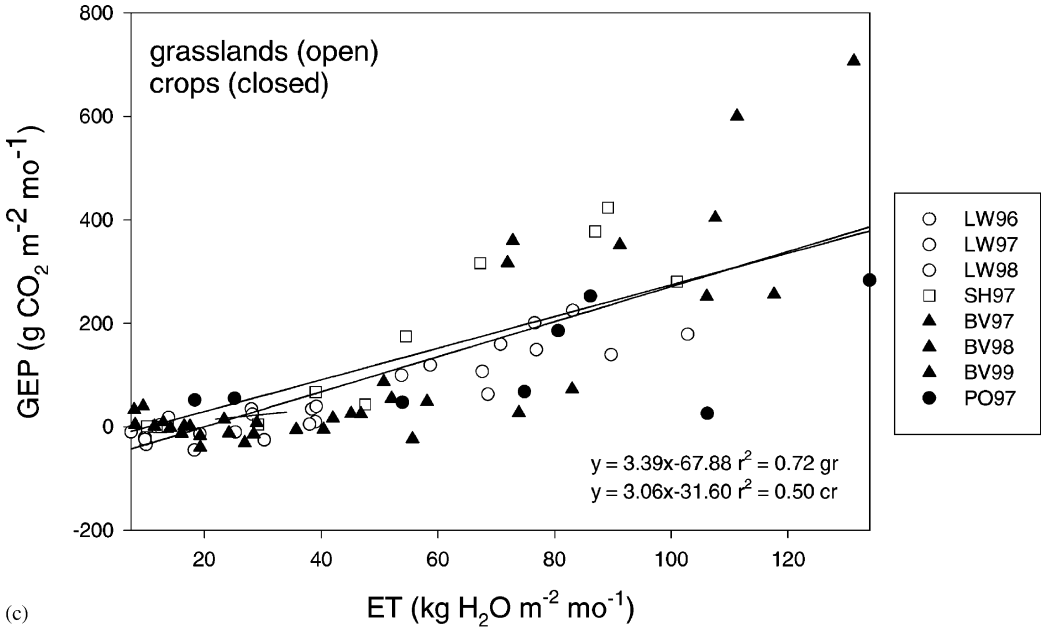
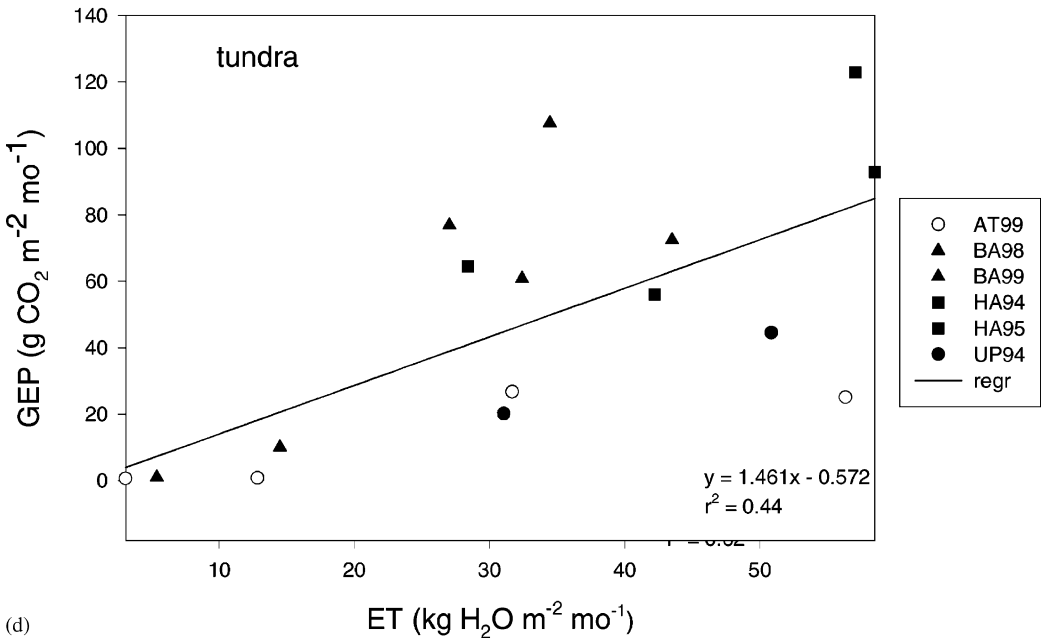


Fig. 6. Monthly GEP increased with ET in: (a) evergreen coniferous forests, where black symbols are boreal forests; (b) deciduous broadleaf forests, where gray symbols are poplar, white symbols are beech, and black symbols are oak/maple; (c) grasslands and croplands. (d) The correlation was weaker for tundra vegetation. (e) Pooled data show that the slope was similar across biomes.



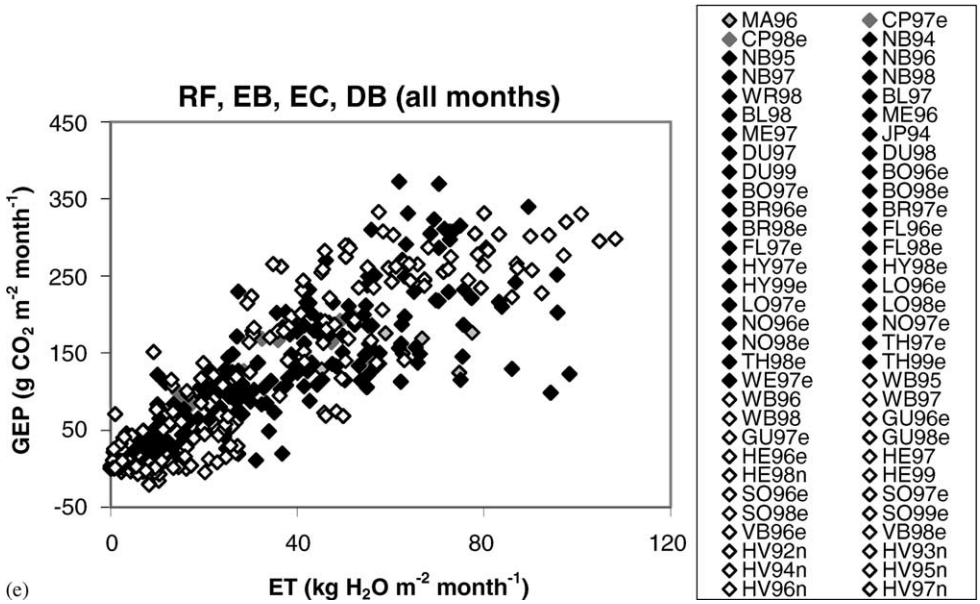
(c)



(d)

Fig. 6. (*Continued*).

that when LAI is less than about 5–6, canopy transpiration is proportional to LAI (Granier et al., 2000b). For a subset of flux sites at which we measured above- and below-canopy ET, the proportion of total ET that evaporated from the forest floor increased as leaf area decreased (Fig. 7). Applying the CANVEG process model, which includes turbulent transport, radiative transfer, and a biochemical model of photosynthesis,



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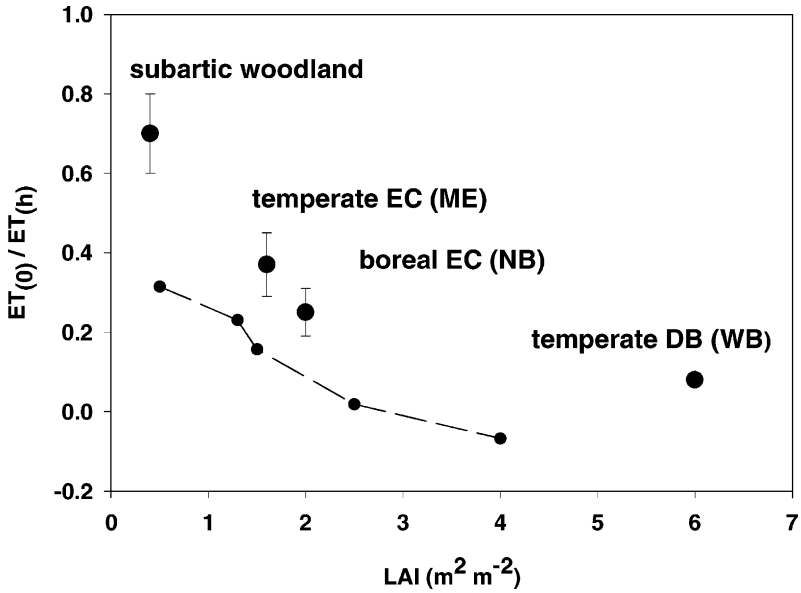


Fig. 7. The proportion of total ET that was evaporation from soil surfaces increased as LAI decreased. Site symbols, defined in Table 1 are given in parenthesis. Vegetation types include a temperate evergreen coniferous forest (EC), a boreal evergreen forest (EC), and a temperate deciduous broadleaf forest (DB). The ET and LAI values for Walker Branch (WB) were calculated from summer values at full leaf (Wilson et al., 2000b).

resulted in a similar relationship for the ponderosa pine site (Law et al., 2001b). Although this is not a functional relationship, it is useful to demonstrate that it can be inappropriate to model evaporation as a constant fraction of precipitation or of total ET throughout the year.

Monthly ecosystem WUE, calculated from GEP divided by ET, decreased with increasing VPD in the

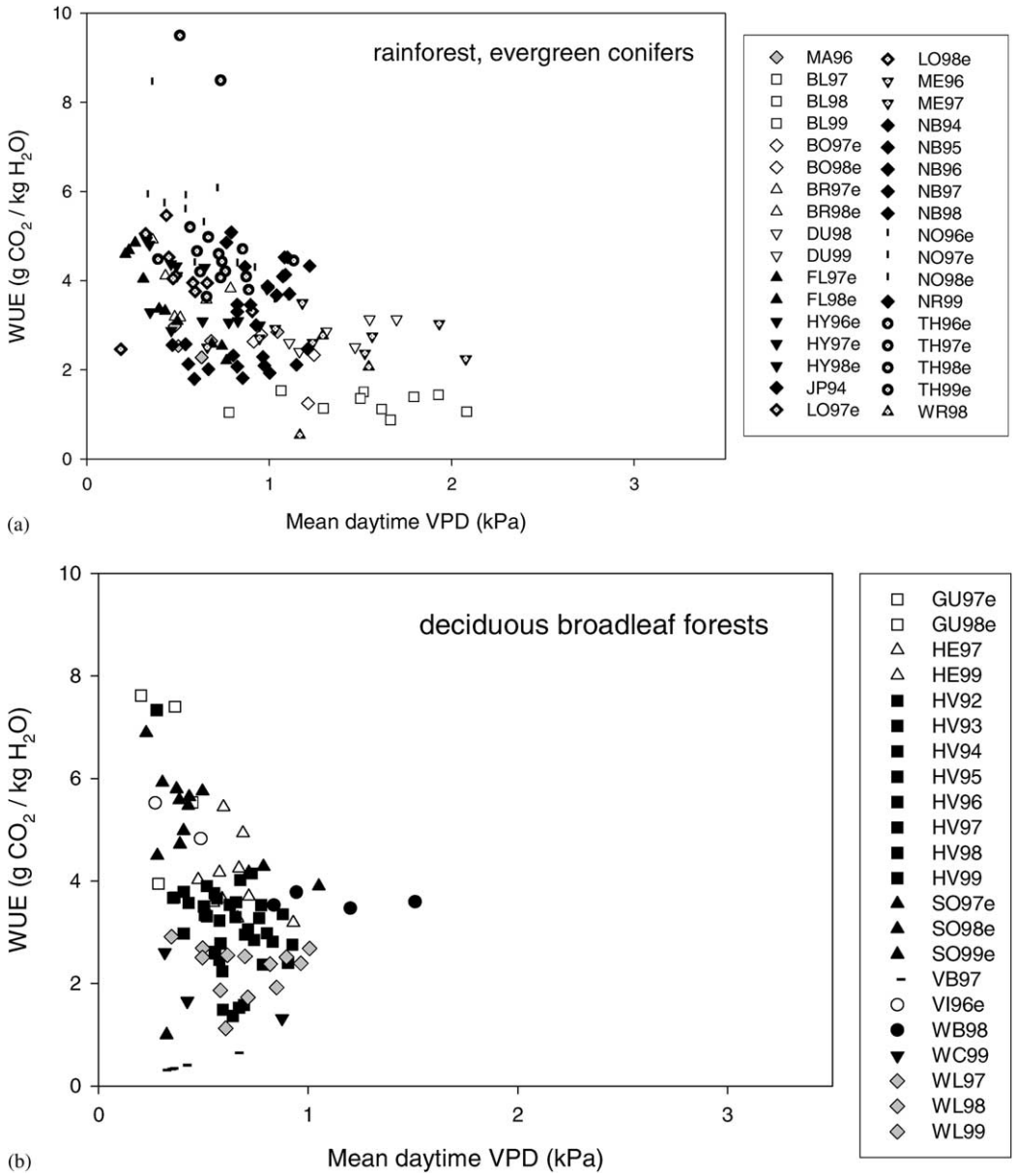
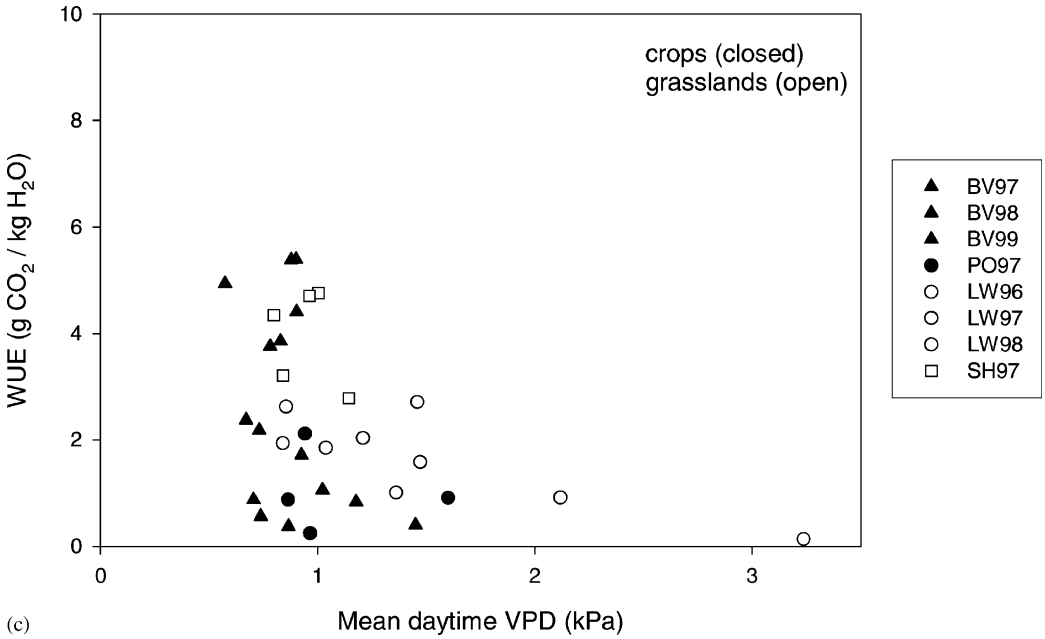


Fig. 8. (a) Monthly water use efficiency (WUE = GEP/ET in g CO_2/kg H_2O) decreased as mean daytime VPD increased in May–September for evergreen coniferous forests (boreal forests: black symbols), and in October–March in a rainforest. (b) Monthly WUE versus mean monthly VPD in deciduous broadleaf forests, and (c) crops (CR) and grasslands (GR).



(c)

Fig. 8. (*Continued*)

summer months (May–September; Fig. 8), but the relation was not as strong for deciduous broadleaf forests (e.g., HV; see Table 1) and a boreal forest (NB; see Table 1), which did not experience VPD values as high as those of other vegetation types. Crops and grasslands were not as efficient as forests at high VPD, as previous studies suggested (Richards and Condon, 1993; Jones, 1992). Weekly means for all sites from May to September showed that WUE reached consistently low values at VPD greater than ~1.5 kPa. At a semi-arid ponderosa pine site (ME; see Table 1), we found that daily ET varied little in summer (~1.6–1.7 mm per day), yet GEP decreased by about 1 g C per day with 1 kPa increase in mean daytime VPD (Anthoni et al., 1999). Although leaf-level experiments indicate that stomatal closure causes a proportionately greater decrease in transpiration than in photosynthesis because of additional diffusive resistances of CO_2 (Cowan, 1982), other studies suggest that when water availability or hydraulic capacity of the whole plant system is limited, stomata adjust to maintain a sustainable water flow and minimize the possibility of xylem cavitation (Mencuccini and Grace, 1996), thereby reducing photosynthesis. This could explain why GEP decreased more than ET at high VPD. Goulden et al. (1997) and Jarvis et al. (1997) found little to no response of GEP to VPD in boreal coniferous forests. At the NB boreal coniferous forest (Table 1), Goulden et al. (1997) observed that the seasonal trends in photosynthesis over 3 years of measurements appeared to be influenced more by phenology than by short-term changes in environmental conditions. Thus, the general trend of decreasing WUE with increasing VPD is limited to the summer growing season for temperate vegetation, whereas temperature and phenology dominate responses in colder climates and during the rest of the year in other regions.

4. Conclusions

We evaluated GEP, NEE, R_e, and LE at temporal scales of weeks, months, and years for sites representing different biomes. Although these responses to climate are relatively short-term, they include the effects of long-term climatic conditions and land use on vegetation type and LAI.

Ecosystem respiration was poorly correlated with mean annual temperature and mean growing season

temperature, even though studies at individual sites showed strong correlations with temperature at shorter temporal scales, and respiration within vegetation type was sensitive to temperature on a monthly scale. Annual GEP was more sensitive to annual temperature than to site water balance, which controls the potential leaf area available for photosynthesis over the long-term, as observed along strong climatic gradients. The slope of the relation between monthly GEP and ET was very similar across vegetation types, however, indicating that physiological processes controlling water loss during carbon uptake reach a sustainable balance through the year. Perhaps this phenomenon is also influenced at the ecosystem level by competition for resources (e.g., self-thinning law in forests, whereby competition for resources limits plant density to a sustainable level).

Studies suggest that disturbance history has a large effect on NEE, compared with inter-annual differences in climate or differences in atmospheric CO_2 (Thornton et al., 2002; Law et al., 2001c; Cohen et al., 1996; Grier and Logan, 1977). Thus, it is important to evaluate the influence of processes on net carbon uptake in terms of developmental stage and disturbance history over longer time frames. Studies addressing this issue are in progress as part of FLUXNET (e.g., CarboAge in Europe; studies in Oregon, North Carolina, and California).

Acknowledgements

We thank the numerous scientists, students, and technicians involved in data collection and analysis at the FLUXNET sites; the agencies that fund the projects (European Union, US Department of Energy Office of Biological and Environmental Research (DOE/BER), National Aeronautics and Space Administration (NASA), and the Multi-agency Program on Terrestrial Ecology for Global Change (TECO)); and the program managers and directors involved in FLUXNET, including Roger Dahlman, Jerry Elwood, and Ruth Reck (US DOE), and Diane Wickland (NASA). The FLUXNET data archive provided the half-hourly data sets containing information on site characteristics for our analyses.

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