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Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements

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Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements

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Abstract

Differences in the seasonal pattern of assimilatory and respiratory processes are responsible for divergences in seasonal net carbon exchange among ecosystems. Using FLUXNET data (http://www.eosdis.ornl.gov/FLUXNET) we have analyzed seasonal patterns of gross primary productivity (F_{GPP}), and ecosystem respiration (F_{RE}) of boreal and temperate, deciduous and coniferous forests, Mediterranean evergreen systems, a rainforest, temperate grasslands, and C_3 and C_4 crops. Based on generalized seasonal patterns classifications of ecosystems into vegetation functional types can be evaluated for use in global productivity and climate change models. The results of this study contribute to our understanding of respiratory costs of assimilated carbon in various ecosystems.

Seasonal variability of F_{GPP} and F_{RE} of the investigated sites increased in the order tropical < Mediterranean < temperate coniferous < temperate deciduous < boreal forests. Together with the boreal forest sites, the managed grasslands and crops show the largest seasonal variability. In the temperate coniferous forests, seasonal patterns of F_{GPP} and F_{RE} are in phase, in the temperate deciduous and boreal coniferous forests F_{RE} was delayed compared to F_{GPP}, resulting in the greatest imbalance between respiratory and assimilatory fluxes early in the growing season.

F_{GPP} adjusted for the length of the carbon uptake period decreased at the sampling sites across functional types in the order C_4 crops, temperate and boreal deciduous forests (7.5–8.3 g C m^{-2} per day) > temperate conifers, C_3 grassland and crops (5.7–6.9 g C m^{-2} per day) > boreal conifers (4.6 g C m^{-2} per day). Annual F_{GPP} and net ecosystem productivity (F_{NEP}) decreased across climate zones in the order tropical > temperate > boreal. However, the decrease in F_{NEP} with latitude was greater than the decrease in F_{GPP}, indicating a larger contribution of respiratory (especially heterotrophic) processes in boreal systems.
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Keywords: Season length; Gross primary production; Ecosystem respiration; FLUXNET; EUROFLUX; AmeriFlux; eddy covariance

1. Introduction

Ecosystem CO_2 exchange is comprised of fluxes associated with assimilatory and respiratory processes. Timing and amplitude of these components determine the seasonal pattern of net CO_2 flux (Randerson et al., 1999; White et al., 1999; Cramer et al., 1999). While at temperate and high latitudes the period for assimilation is usually restricted by temperature and moisture, respiratory processes continue throughout the year. Major factors affecting the seasonal course and amount of ecosystem gross primary production (F_{GPP}), are seasonal differences in leaf-area index, physiological capacity, meteorological conditions, and the length of the growing season. Ecosystem respiration (F_{RE}) as the sum of heterotrophic respiration (F_{RH}), and autotrophic respiration (F_{RA}), is typically dominated by disparate factors. The activity of soil microbes contributes to F_{RH}, and is strongly regulated by soil temperature and moisture status (Edwards, 1975; Lloyd and Taylor, 1994; Davidson et al., 1998; Xu and Qi, 2001). While F_{RA} may be maintained over the course of the year, the partitioning of autotrophic respiration varies seasonally as the relative roles of growth and maintenance respiration change. Periods of microbial activity does not necessarily coincide with those where green plants are photosynthetically active, as microbial activity depends on suitable meteorological conditions as well as on substrate availability and quality. Clearly, it is the interplay between photosynthetic and microbial active seasons, that determines the seasonal pattern, phasing and amplitude of ecosystem energy and material fluxes.

The balance between respiratory and assimilatory processes is likely to be affected as a result of climate change (Houghton et al., 1996). Systematic changes in the length of the growing season (Keeling et al., 1996a; Myneni et al., 1997; Hasenauer et al., 1999; Menzel and Fabian, 1999; Randerson et al., 1999; Keyser et al., 2000; Baldocchi et al., 2001) indicate an extension of the period favorable for assimilation. The influence of climate on respiratory processes is generally more complicated. Soil respiration, for example, is strongly coupled to soil temperature (Raich and Schlesinger, 1992; Lloyd and Taylor, 1994), however, in some ecosystems microbial activity is affected by soil moisture (e.g., Hanson et al., 1993; Fliebach et al., 1994; Law et al., 2000). Soil models typically predict an exponential increase of soil respiration with temperature, but with a secondary limitation by the

quantity and quality of the substrate for microbial activity (Rastetter et al., 1992). The feedbacks between temperature, moisture availability, and substrate properties seem to control the overall rate of soil respiration (Raich and Tufekciogul, 2000). In addition, temperature increases due to climate change are not evenly distributed over the time of the day with greater increases observed during night than in the day-time (Easterling et al., 1997). Shifts in the relative contribution of assimilation and respiration to total fluxes could affect future ecosystem carbon sequestration potentials, and the stability of stored carbon (Alward et al., 1999). On the other hand, potential shifts in photosynthetic and microbial activities could reduce or reverse the benefits of increased growing season length to carbon sequestration.

At temperate and high latitudes carbon balances of terrestrial ecosystems undergo strong seasonal fluctuations. Growing season length strongly affects annual net ecosystem productivity F_{NEP} ($=F_{GPP} - F_{RE}$), (Black et al., 1996, 2000; Goulden et al., 1998; Baldocchi et al., 2001; Meyers, 2001), and ecosystem net primary production, F_{NPP} ($=F_{GPP}-F_{RA}$) (Schulze et al., 1999). Model analyses suggest major impacts of growing season length on F_{NPP} (Field et al., 1998; White et al., 1999; Jackson et al., 2000). Average F_{NPP}, for example, varies among biomes between 0 and 1.2 kg C m^{-2} per year (Bergen and Dobson, 1999; Cramer et al., 1999; Goetz et al., 1999; Jiang et al., 1999; Nemry et al., 1999), but differences in F_{NPP} are much smaller when adjusted for the length of the growing season. These studies address seasonal fluctuations of the net fluxes, F_{NEP}, or F_{NPP}, but the component fluxes, F_{GPP} and F_{RE}, often have dissimilar periods of activity. For instance, F_{GPP} is strongly dependent on light during the growing season when temperature is adequate for growth, whereas F_{RE} is strongly dependent on temperature and moisture. Over the season light, temperature and moisture are out of phase, and this differs with latitude. Hence these drivers will affect net ecosystem carbon exchange (F_{NEE}) differently as they force F_{GPP} and F_{RE} differently (Randerson et al., 1999). Consequently, we need to understand primarily the factors that influence the seasonality of the component fluxes, F_{RE} and F_{GPP}, and govern the seasonal patterns of net fluxes.

Tower-based observing systems based on micrometeorological techniques provide means to directly measure F_{NEE}, which differs from F_{NEP} by the amount of carbon exported from the system via run-off or harvest. Valentini et al. (2000) used data from a network of tower observations to obtain F_{RE} and F_{GPP} by an extrapolation of site-specific exponential relationships between nocturnal fluxes and soil temperature into the day to calculate continuous records of F_{RE}. This approach allows us to investigate seasonal phasing and amplitudes of ecosystem respiration and assimilation. We make use of FLUXNET (http://www.eosdis.ornl.gov/FLUXNET), a data base with ecosystem CO_2 flux (F_{NEE}) and meteorological data obtained from tower-based systems between years 1992 and 2000. The sites on the European and American continents include deciduous and evergreen forests, grassland and crops, and cover a wide range of climatic zones, from boreal to tropical. The analysis provides valuable insight into the seasonality of respiration and assimilation for sites in a variety of ecotones, and better understanding of the processes that regulate F_{NEE}. This work contributes to our understanding of how well seasonal phasing and amplitudes of respiratory and assimilatory processes are currently represented in carbon cycle and soil–vegetation–atmosphere transfer (SVAT) models.

2. Methods

2.1. The data base and sites

FLUXNET (http://www.eosdis.ornl.gov/FLUXNET) hosts a data base of continuous measurements of ecosystem carbon and energy exchange, key meteorological variables and ancillary data describing location, vegetation and climate of the sites. The data sets cover multiple years (1992–2000) of flux tower measurements from the AmeriFlux (23 sites) and EUROFLUX (16 sites, Valentini et al., 2000; Valentini, 2002) projects. From these we selected 35 sites (Table 1), where night-time turbulence and hence F_{RE} could be assessed (details below). Mass and energy fluxes are measured with the eddy covariance technique (for details see, e.g., Aubinet et al., 2000). The data undergo quality assurance, and missing half-hourly averages are filled using standardized methods to provide complete data sets (Falge et al., 2001).

Table 1
Vegetation type classification of 35 sites from the EUROFLUX and AmeriFlux projects[a]

Functional vegetation type	Site	Abbreviation	State/country
Temperate coniferous forests	Aberfeldy[b]	AB	UK
	WeidenBrunnen[b]	WE	Germany
	Tharandt[b]	TH	Germany
	Loobos[b]	LO	The Netherlands
	Brasschaat[b]	BR	Belgium
	Wind River[c]	WR	WA/USA
	Howland[c]	HL	ME/USA
	Metolius[c]	ME	OR/USA
	Duke Forest[c]	DU	NC/USA
High altitude coniferous forests	Niwot Ridge[c]	NR	CO/USA
Boreal coniferous forests	North Boreas[c]	NB	Man./Canada
	Flakaliden[b]	FL	Sweden
	Norunda[b]	NO	Sweden
	Hyytiala[b]	HY	Finland
Temperate deciduous forests	Vielsalm[b]	VI	Belgium
	Soroe[b]	SO	Denmark
	Hesse[b]	HE	France
	Harvard[c]	HV	MA/USA
	WalkerBranch[c]	WB	TN/USA
Cold temperate deciduous forests	Park Falls/WLEF	WL	WI/USA
	Willow Creek[c]	WC	WI/USA
Boreal deciduous forests	Gunnarsholt[b]	GU	Iceland
Maritime/Mediterranean evergreen forests	Bordeaux[b]	BO	France
	Castelporziano[b]	CP	Italy
	Sky Oaks young [c]	Skyoung	CA/USA
	Sky Oaks old [c]	Skold	CA/USA
	Blodgett Forest[c]	BL	CA/USA
Rainforest	Manaus[c]	MA	Brazil
Grasslands	LittleWashita[c]	LW	OK/USA
	Shidler[c]	SH	OK/USA
	Risoe[b]	RI	Denmark
Crops	Bondville[c]	Bvcorn	IL/USA
	Bondville[c]	Bvsoybean	IL/USA
	Ponca[c]	PO	OK/USA
	Soroe[b]	Sowheat	Denmark

[a] For more information on these sites see Falge et al. (2002).
[b] EUROFLUX projects.
[c] AmeriFlux projects.

2.2. The algorithms

2.2.1. Estimates of F_{RE} and F_{GPP}

Ecosystem respiration, F_{RE}, is measured directly at the towers during night-time periods with strong turbulence (typically indicated by high surface momentum flux, e.g., Goulden et al., 1996), and was extrapolated to other periods by using exponential regressions of measured F_{RE} with soil temperature. Alternative methods to estimate F_{RE} for periods when it was not directly measured includes estimates from biogeochemical or SVAT models (e.g., Baldocchi et al., 2000), from chamber measurements extrapolated to the stand scale (Law et al., 1999; Janssen

et al., 2001; Xu et al., 2001), or estimates derived from the regression of day-time F_{NEE} against photosynthetically active radiation (PAR) (e.g., Suyker and Verma, 2001). For the exponential regression here an Arrhenius equation (Eq. (1)) in the form reported by Lloyd and Taylor (1994) was used.

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

where $F_{RE,\ T_{ref}}$, is the ecosystem respiration rate at T_{ref} (we used 283.16 K) and E_a the activation energy in J mol^{-1} are fitted site-specific parameters, R the gas constant (8.134 J K^{-1} mol^{-1}), and T_K is the soil temperature in a depth of 5 cm. The parameter $F_{RE,Tref}$ was evaluated for gliding 30-day period starting 1 January but E_a was kept constant over the entire year. This might not be valid, as we expect changes in E_a due to changes in soil moisture conditions and the effects of growth and maintenance respiration. Yet, the overall scatter typically found in the relationship between night-time T_K and F_{RE} determined by eddy covariance (e.g., Goulden et al., 1996) prevented us from analyzing such effects. For more details on the quality of the fits see Appendix A (see Table 4). The derived parameter sets were applied over the entire year to obtain a continuous record of half-hourly data. Values of F_{GPP} were calculated as the difference between F_{RE} and F_{NEE}. For daily values of F_{RE} and F_{GPP} the half-hourly results were summed. To address errors in our F_{RE} (and subsequently F_{GPP}) estimates, we compared the estimates to values derived from light responses (hyperbolic relationship between F_{NEE} and light, using Eq. (1) of Suyker and Verma, 2001).

2.2.2. Maximum diurnal ecosystem respiration and gross primary production

We used diurnal maximum fluxes, F_{RE} and F_{GPP}, to assess the seasonal changes in rates of ecosystem respiration and assimilation. We calculated mean diurnal cycles by bin-averaging the 30 min tower flux data for intervals of 15 days (see Falge et al., 2002, Eq. (1)). This time interval was chosen because a variety of ecosystems fluxes show a spectral gap at this period (Baldocchi et al., 2001). Missing data were filled by look-up table methods based on meteorological conditions (temperature and radiation for F_{GPP}, temperature for F_{RE}, see Falge et al., 2001). This type of gap filling was shown to introduce no bias errors (Falge et al., 2001). Bin-averaging reduced sampling errors by $1/\sqrt{15}$ (Moncrieff et al., 1996), and the procedure resulted in 350 (=365 − 15) mean diurnal courses per year. The maximum values of F_{RE} and F_{GPP} for each diurnal course were determined. Estimating averages for 30-day period using Eq. (1) reduces random errors of one-point eddy covariance measurements by a factor of $1/\sqrt{30}$ or 0.183, resulting in uncertainties of ±3% for the mean of a 30-day period if the random error is assumed to be 15%. This does not take into account systematic errors potentially observed with eddy covariance at night or on unfavorable terrain. For a more detailed review of uncertainty estimates, see Goulden et al. (1996) or Moncrieff et al. (1996).

3. Results

As F_{GPP} is calculated from the sum of F_{RE} and F_{NEP}, errors in F_{RE} affect the magnitude of F_{GPP} estimates. Therefore we compared our estimates of F_{RE} to values derived from the light response of F_{NEP} during the growing season (April to mid September), where a typical hyperbolic relationship between F_{NEP} and light can be observed. The methods compare well for most sites (Fig. 1): a linear regression yields a slope of 0.94 and an intercept of 0.25 g C m^{-2} per day. Excluding fluxes taken at night when evaluating light responses of F_{NEP}, the above linear comparison has a similar slope of 1.00 and intercept of −0.17 g C m^{-2} per day but more scatter (data not shown). Three boreal sites (Norunda, North Boreas, Gunnarsholt), and two crop sites (Bondville, Soroe-Wheat) were not included in the linear regression. We also excluded the prairie site (Shidler), which yielded a 20% smaller estimate when F_{RE} is derived from light responses, a similar result as reported in Suyker and Verma (2001). In particular, it seems the methods do not compare well in boreal and grass or crop ecosystems. This could be due to low leaf-area indices with dead material and/or bare soil intercepting photons in those systems, reducing photosynthetic light use efficiency. Also, these systems (particularly Norunda) are losing lots of carbon from below ground and other carbon pools, and deviations in the estimates of F_{RE} eventually reveal the relative differences between short term autotrophic carbon loss versus longer term heterotrophic carbon loss.

Seasonal pattern of maximum and mean diurnal F_{GPP} and F_{RE} are shown for four sites in Fig. 2.

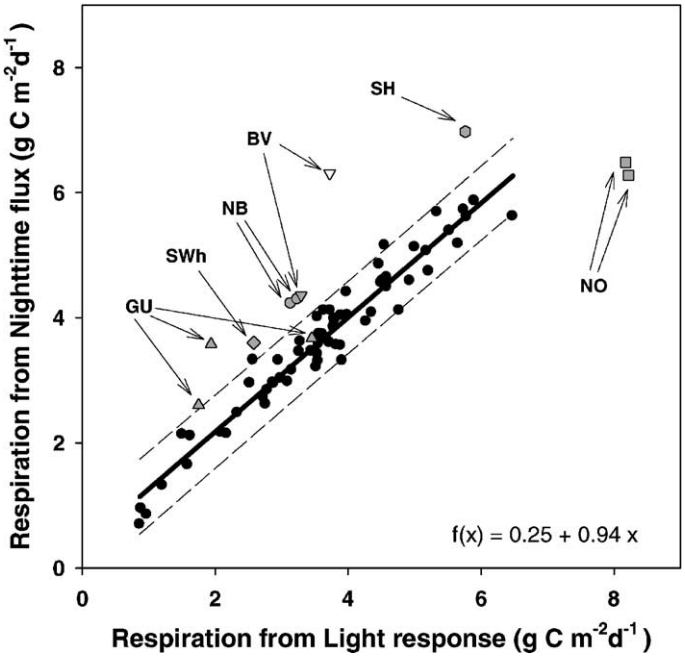

Fig. 1. Ecosystem respiration (F_{RE}), calculated from light response relationships (Eq. (1) in Suyker and Verma (2001)) compared to the values derived from exponential regressions between soil temperature and night-time fluxes under turbulent conditions (Eq. (1)). Data represent average daily sums for all days of the growing season where both methods could be applied. Three boreal sites (NO: Norunda; NB: North Boreas; GU: Gunnarsholt), two crop sites (BV: Bondville; SWh: Soroe-Wheat) and the prairie site (SH: Shidler) are not included in the linear regression.

Assimilation is active year-round in the temperate coniferous and the evergreen broad-leaf forest, and shows a very confined season in the deciduous and the boreal forest. With the exemption of the boreal coniferous forest—we find correspondence between the amount of assimilation and respiration, high respiration at high assimilation and low respiration at low assimilation rates. The seasonal course of mean F_{GPP} shows similar patterns, however the differences between mean F_{GPP} and F_{RE} are smaller than for diurnal maximum fluxes. Mean F_{GPP} and F_{RE} are mostly out of phase for the boreal conifers, but the temperate and Mediterranean systems show again the compensatory behavior of F_{GPP} and F_{RE}.

Fig. 3 shows maximum F_{GPP} for the temperate and boreal deciduous and coniferous forests. F_{GPP} could not be calculated for all sites due to incomplete seasonal F_{RE}. Site specific data were smoothed by applying a 10-day moving average, and normalized to the maximum observed value during the year. Absolute maximum and minimum values and the corresponding day of the year are given in Table 2. We averaged the data for each site for all available years to reduce the sensitivity of the results to occasional large gaps in the data and to depict biome specific patterns rather than inter-annual variability. Seasonal courses of maximum F_{GPP} of the temperate and boreal forest sites show the pattern we found for net uptake (see Falge et al., 2002), temperate conifers with the longest, boreal deciduous with the shortest, and temperate deciduous and boreal coniferous forests with intermediate and indeed very similar assimilation periods. The temperate coniferous forests and Vielsalm (VI), a mixed forest, show assimilation potential even in winter. The low assimilation rates at Brasschaat (BR) in April and May are probably due to anthropogenic influences (CO_2 sources from residential areas). The assimilation potential of the high altitude coniferous forest site (Niwot Ridge, NW) is similar to the temperate deciduous forest sites, clearly pointing to a delayed phenology for conifers at high elevations.

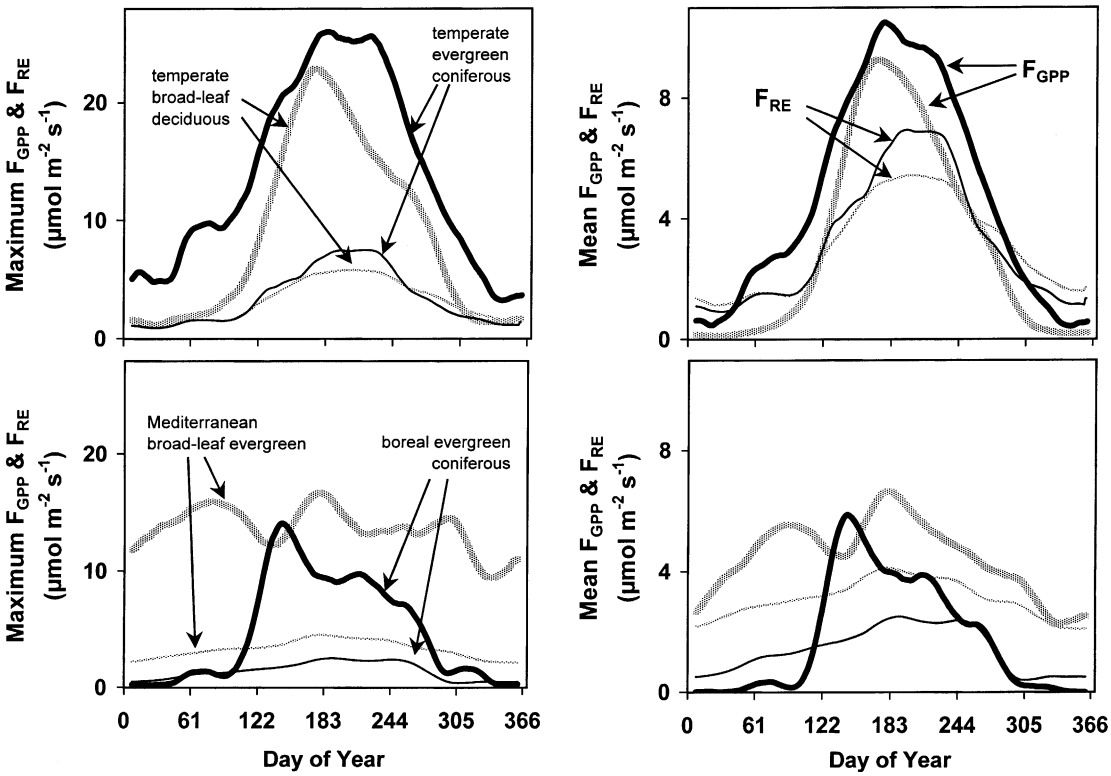

Fig. 2. Seasonal development of maximum mean diurnal ecosystem gross primary production (F_{GPP}), and maximum diurnal ecosystem respiration (F_{RE}), from 15-day bin-averaged data. Temperate forest sites are in the upper panel (Tharandt and Soroe), and Mediterranean and boreal are in the lower panel (Castelporziano and Flakaliden).

The results for the seasonal trends of maximum F_{RE} are shown in Fig. 4. In general, they resemble the patterns we described for maximum night-time carbon release in Falge et al. (2002). However, there seems to be a more gradual transition between the patterns of the temperate conifers, temperate deciduous, and the boreal conifers, as we analyze F_{RE} during the entire day, i.e., maximum values are likely to occur during day-time when temperatures are higher. In general, the seasonal pattern in F_{RE} reveals a large influence of climate (temperate versus boreal), whereas the life-form (deciduous or coniferous) seems to be less relevant for the seasonality of respiratory processes.

Figs. 5 and 6 summarize seasonal patterns of F_{GPP} and F_{RE} for the sites of the remaining functional types, grassland, crops, maritime/Mediterranean ecosystems, and a rainforest. Maximum F_{GPP} of the evergreen maritime and Mediterranean forests reflects their year-round assimilatory activity (Fig. 5), and maximum F_{RE} never drops below 25% of the maximum observed value during the season. However, drought periods are likely to affect F_{RE} during late spring (CP), or summer (BL, BO). For the temperate grassland sites the phasing of maximum F_{RE} (Fig. 6) corresponds well with the patterns observed in temperate deciduous forests, however the amplitudes differ: maximum F_{RE} in the forests (Fig. 4) does not decline to almost 0 in winter, as it is found for the grasslands. Crop sites often develop a second maximum in F_{GPP} after the harvest due to inter-crops or weeds, and several maximums in F_{RE} evidently following management practices (Fig. 6).

Summarizing Figs. 3–6, the seasonal patterns observed in Falge et al. (2002) are reflected in the results for F_{GPP} and F_{RE} and grouped for the sites in the above functional types. Temperate deciduous and

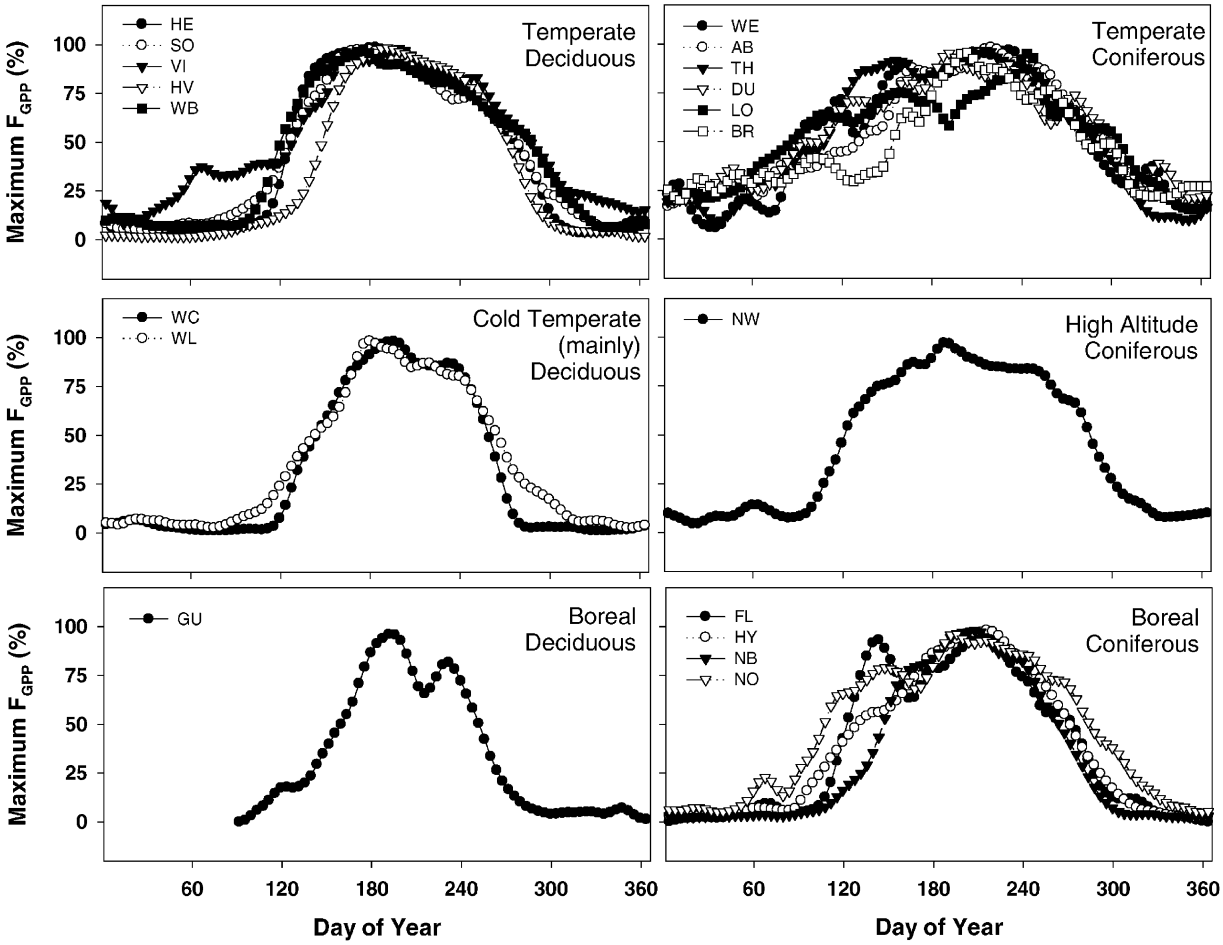

Fig. 3. Seasonal development of maximum diurnal F_{GPP}, for selected sites from Table 1, temperate, cold temperate, and boreal deciduous forests (left panels), and temperate, high altitude, and boreal coniferous forests (right panels). Data are normalized such that the maximum observed value equals 100%. Absolute maximum values are given in Table 2.

boreal coniferous forest sites comprise one class in terms of the seasonal phase and amplitude of F_{GPP}, whereas temperate coniferous sites show a prolonged carbon uptake period together with smaller amplitude. In contrast, the seasonal course of F_{RE} of the temperate deciduous forest sites matches the pattern found for the temperate conifers, whereas the phasing of F_{RE} of boreal conifers is shorter and the amplitude larger. Fig. 7 shows the difference between seasonal maximum (set to 100%) and minimum F_{GPP} (values of sampling sites averaged within vegetation functional types). Minimum F_{GPP} amounts to 75% of the maximum in the tropical system, 30% in the maritime/Mediterranean evergreen systems, 12% in the temperate coniferous systems, and 0–4% in the other systems as boreal forest sites, temperate deciduous sites, grasslands and crops. Similarly, minimum seasonal rates of F_{RE} amounts to 95% of maximum F_{RE} in the tropical, 35% in the maritime/Mediterranean, 14–17% in the temperate forest sites (deciduous and coniferous), 9% in the boreal coniferous forests, and 4–6% in the boreal deciduous forest, grassland and crop sites.

In Falge et al. (2001) we used the ratio between F_{GPP} and F_{RE} ($z = F_{GPP}/F_{RE}$) to evaluate the relative contribution of carbon exchange processes to the

Table 2
Seasonal maximum and minimum of F_{GPP} and F_{RE}, together with the day of the year, where maximum and minimum rates occur, for 29 sites from the EUROFLUX and AmeriFlux projects[a]

Site	F_{GPP}		F_{RE}	
	Seasonal maximum (μmol CO_2 m^{-2} s^{-1})	Seasonal minimum (μmol CO_2 m^{-2} s^{-1})	Seasonal maximum (μmol CO_2 m^{-2} s^{-1})	Seasonal minimum (μmol CO_2 m^{-2} s^{-1})
Temperate coniferous forests				
Aberfeldy[b]	16.0 (216)	2.5 (1)	5.3 (225)	0.7 (3)
WeidenBrunnen[b]	18.3 (232)	0.7 (36)	7.3 (230)	1.4 (37)
Tharandt[b]	25.3 (216)	2.0 (34)	6.9 (215)	1.0 (35)
Loobos[b]	24.0 (246)	3.5 (351)	5.3 (177)	1.0 (7)
Brasschaat[b]	20.2 (202)	3.4 (12)	16 (172)	2.1 (72)
Duke Forest[c]	24.5 (191)	4.6 (8)	3.6 (206)	1.0 (65)
High altitude coniferous forests				
Niwot Ridge[c]	15.1 (186)	0.5 (23)	6.3 (185)	1.0 (353)
Boreal coniferous forests				
North Boreas[c]	18.1 (210)	0.4 (352)	12.8 (211)	0.3 (28)
Flakaliden[b]	13.2 (219)	0.0 (6)	4.1 (212)	0.5 (12)
Norunda[b]	30.4 (191)	1.4 (7)	8.6 (187)	1.2 (41)
Hyytiala[b]	13.1 (219)	0.2 (351)	4.0 (213)	0.3 (43)
Temperate deciduous forests				
Vielsalm[b]	21.5 (196)	1.6 (7)	21.5 (196)	1.6 (7)
Soroe[b]	25.3 (175)	1.1 (27)	6.8 (208)	1.2 (34)
Hesse[b]	24.8 (184)	0.6 (14)	7.4 (223)	0.8 (35)
Harvard[c]	25.0 (190)	0.4 (49)	4.7 (191)	1.0 (37)
Walker Branch[c]	29.9 (176)	1.8 (332)	3.9 (202)	0.4 (33)
Cold temperate deciduous forests				
Park Falls/WLEF[c]	19.6 (178)	0.4 (74)	7.9 (200)	0.3 (363)
Willow Creek[c]	28.3 (190)	0.2 (72)	5.7 (190)	0.5 (22)
Boreal deciduous forests				
Gunnarsholt[b]	23.0 (192)	0.2 (1)	13.6 (183)	0.1 (3)
Maritime/Mediterranean evergreen forests				
Bordeaux[b]	23.8 (159)	7.6 (339)	7.4 (177)	1.8 (29)
Castelporziano[b]	17.5 (178)	8.4 (338)	4.6 (172)	2.1 (4)
Blodgett Forest[c]	23.8 (159)	7.6 (339)	3.3 (343)	0.9 (257)
Rainforest				
Manaus[c]	29.5 (4)	22.3 (189)	7.2 (267)	6.9 (362)
Grasslands				
LittleWashita[c]	14.4 (176)	0.7 (356)	6.6 (181)	0.4 (362)
Shidler[c]	39.2 (182)	0.1 (24)	15.0 (176)	0.3 (14)
Crops				
Bondville[c] C4	60.5 (199)	0.3 (294)	15.8 (180)	0.1 (362)
Bondville[c] C3	27.3 (196)	0.3 (73)	8.7 (182)	0.0 (11)
Ponca[c]	33.5 (124)	1.7 (226)	6.0 (210)	1.4 (22)
Soroe[b]	31.7 (187)	0.2 (25)	10.8 (145)	0.0 (7)

[a] Data are averaged for all available years. Values of $F_{GPP,max}$ and $F_{RE,max}$ are derived as maximum values from a time series of F_{GPP} and F_{RE} using a 15-day running mean filter for each half-hour of the day. Values in parenthesis indicate the day of the year.

[b] EUROFLUX projects.

[c] AmeriFlux projects.

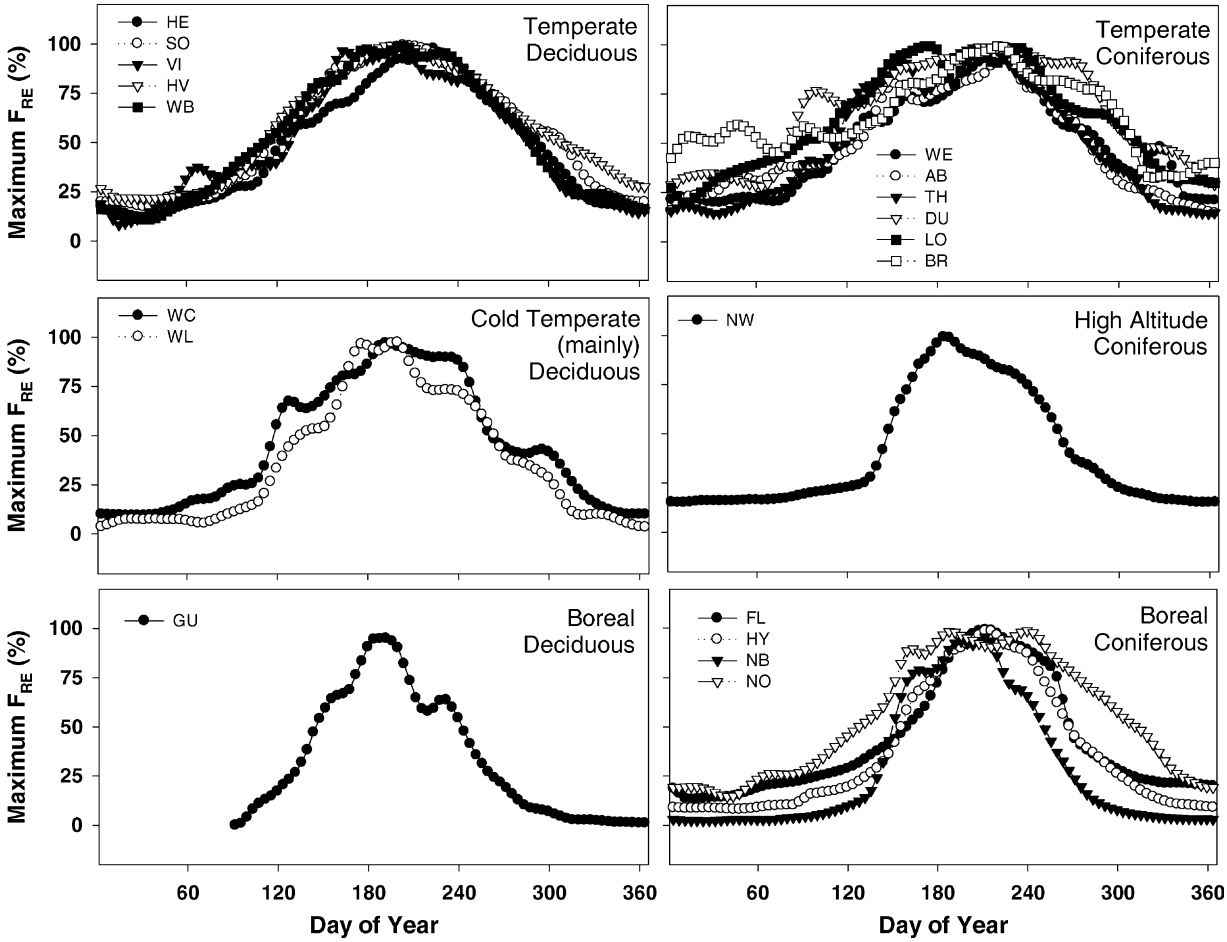

Fig. 4. As in Fig. 3, but for seasonal development of maximum diurnal F_{RE}, for selected sites from Table 1.

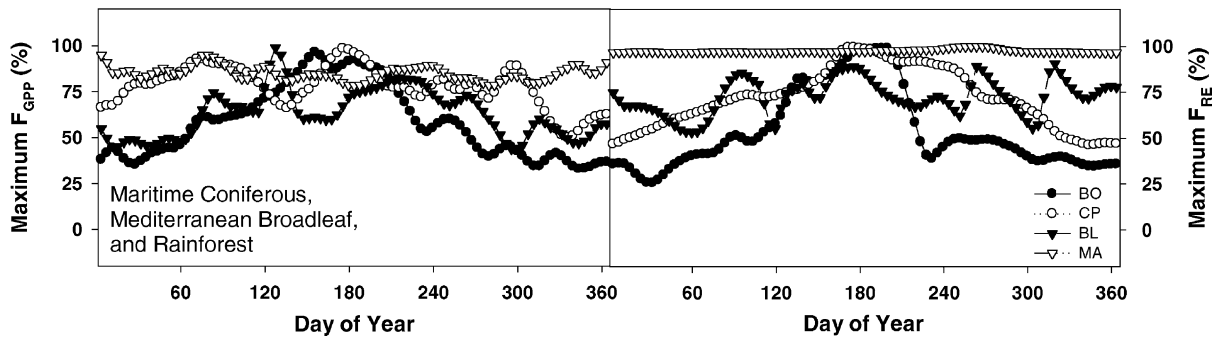

Fig. 5. Seasonal development of maximum diurnal F_{GPP} (left panel), and maximum mean diurnal F_{RE} (right panel), for maritime and Mediterranean evergreen forests from Table 1.

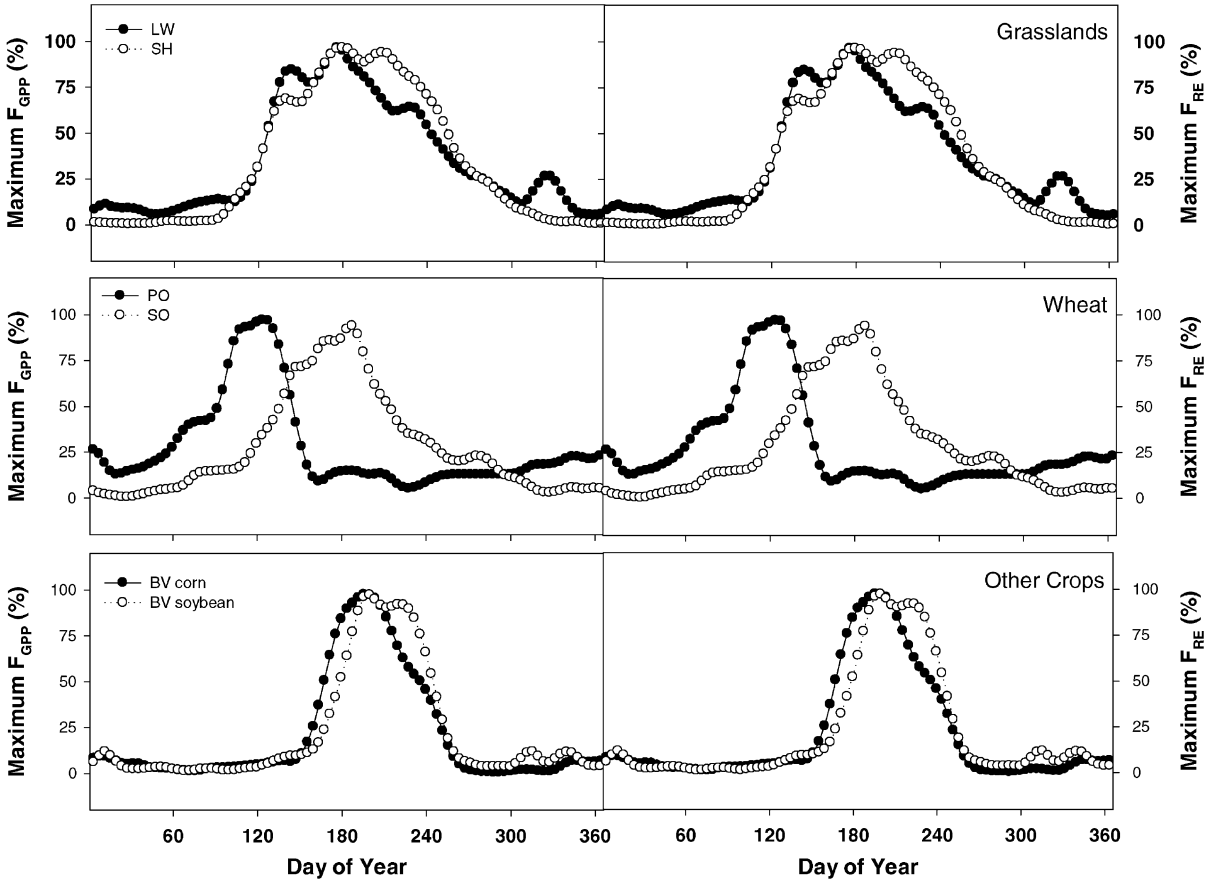

Fig. 6. Seasonal development of maximum diurnal F_{GPP} (left panel), and maximum diurnal F_{RE} (right panel), for grassland and crop ecosystems (Table 1).

total annual exchange. This analysis illustrates what fraction of assimilation is consumed by the plant or supports the activities of heterotrophs in the soil. Values of z below 1 occur when the system becomes a source of CO_2, while $z = 1$ on an annual or decadal basis indicates a system that is in carbon balance ($F_{NEE} = 0$). When F_{GPP} exceeds F_{RE} ($z > 1$) the system is storing carbon, usually observed in young "growing" stages. When F_{GPP} substantially exceeds F_{RE} the system has potential to deprive of free nutrients by accumulating both carbon and available nutrients in (dead) biomass. Considering the close link between soil organic matter decomposition and nutrient cycling, systems with low F_{RH} will likely show negative feedbacks to growth and F_{GPP} or become susceptible to disturbance (e.g., Schulze et al., 1999; Walker et al., 1999; Amiro, 2001). We calculated values of z from monthly sums of F_{GPP} and F_{RE} over the course of the year averaged for all available years for each site (Fig. 8). The length of the period during which z was greater than 1 is a measure of the length of the carbon uptake period (in days, $S_{GPP/RE}$, see Table 3). Carbon uptake periods were longest in the evergreen systems such as Mediterranean and temperate coniferous forests, shorter in the boreal and temperate deciduous forests and native grasslands, and shortest in the crop systems (not shown) and drought stressed rangeland (LW). Values of $z = 2$ (dotted lines in Fig. 8) correspond to $F_{NEP} = F_{RE}$, indicating low overall contribution of F_{RH}, suggesting that autotrophic processes mainly govern ecosystem carbon fluxes, as was observed for the crops, the boreal conif-

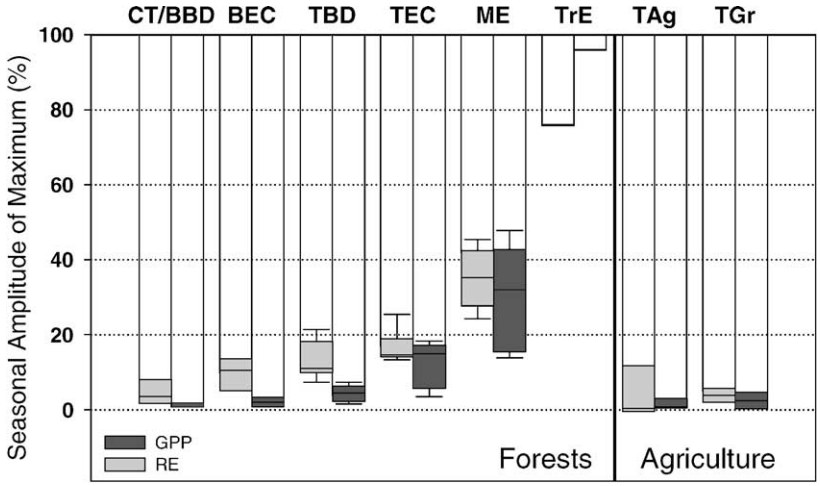

Fig. 7. Seasonal amplitudes of maximum ecosystem gross primary production, F_{GPP} and maximum ecosystem respiration, F_{RE}, grouped by functional type (CT/BBD: cold temperate broad-leaf deciduous; BEC: boreal evergreen conifers; TBD: temperate broad-leaf deciduous; TEC: temperate evergreen conifers; ME: maritime/Mediterranean evergreen forests; TrE: rainforest; TAg: temperate crops; TGr: temperate grasslands). Data are derived by calculating the ratio between minimum and maximum values reported in Table 2 in percentage, and averaged for each functional type. Box charts are used to emphasize total range, and median.

erous sites in spring and for some temperate deciduous and coniferous forests over several months. In the boreal coniferous systems (Fig. 8a), the large z-values in spring reflect physiological activity of the leaves while heterotrophic processes are still slow due to low soil temperatures (Goulden et al., 1998). Low values of z, reflecting low rates of photosynthesis, are found in drought stressed ecosystems (LW and BL, Fig. 8b).

4. Discussion

In this study we presented phasing and amplitude of ecosystem gross primary production (F_{GPP}), and ecosystem respiration (F_{RE}) over the course of the year. Data were obtained from eddy covariance tower networks from sites of a variety of functional vegetation types of the Northern Hemisphere, and a tropical rainforest site. We derived seasonal patterns of photosynthetic and respiratory activity, and investigated ecosystem differences in the ratio of organic carbon consumed (F_{RE}) and produced (F_{GPP}) within the system.

Identification of functional types allows treating groups of vegetation units or species as single entities according to their specific interaction with the environment. The usefulness of this concept depends on the attributes selected for the classification. From a functional perspective, ecosystems could be grouped by their mass and energy exchange or productivity and respiration rates. Applying a more morphologic view, global models of climate change and productivity employ classification schemes by biome or vegetation type, e.g., evergreen needle-leaf forest, deciduous broad-leaf forest (Warnant et al., 1994; Field et al., 1995; Sellers et al., 1996a,b; Kohlmaier et al., 1997). We analyzed seasonal pattern of F_{GPP} and F_{RE} to test the potential to generalize functional characteristics within currently applied classification schemes.

Standard attributes in classification schemes of global models are life-forms (e.g., deciduous or coniferous) and climate (e.g., temperate, boreal). Remarkable parallels were found in seasonal pattern of net ecosystem fluxes (F_{NEP}) within and between groups defined by life-form and climate zone (Falge et al., 2002). In general, the seasonal patterns for F_{GPP} and F_{RE} from the sampling sites reflect the results observed for F_{NEP}. The seasonal patterns of F_{RE} of the temperate deciduous and coniferous forests are similar in length to the active period, while the active season for F_{RE} in the boreal conifers is shorter. In terms of F_{GPP}, in contrary, the temperate deciduous and boreal

coniferous forest sites are similar, whereas the temperate conifers show a longer active season. The seasonal amplitude of maximum rates of F_{GPP} and F_{RE} at the investigated sites increases in the order tropical < maritime/Mediterranean < temperate coniferous < temperate deciduous < boreal evergreen forests < cold temperate and boreal deciduous forests. Again, the temperate and boreal coniferous forests fall in two different classes. Thus, climate has a large impact on the seasonal pattern in F_{RE} while life-form dictates the seasonality of assimilatory processes.

We assessed ecosystem carbon balances by analyzing the ratio between F_{GPP} and F_{RE} ($z = F_{GPP}/F_{RE}$, Falge et al., 2001). When $z > 1$ on an annual or decadal basis the system is storing carbon, when $z = 1$ the system is in carbon balance, and F_{RH} equals F_{NPP}. Typically, the ratio F_{GPP}/F_{RE} was between 1 and 2 during the growing season and below 1 during the dormant period, showing the use of stored carbon during this phase. Sites with prolonged periods of values of 2 ($F_{NEP} = F_{RE}$) and higher could indicate problems during application of the eddy covariance method, as F_{GPP}/F_{RE} will likely be overestimated

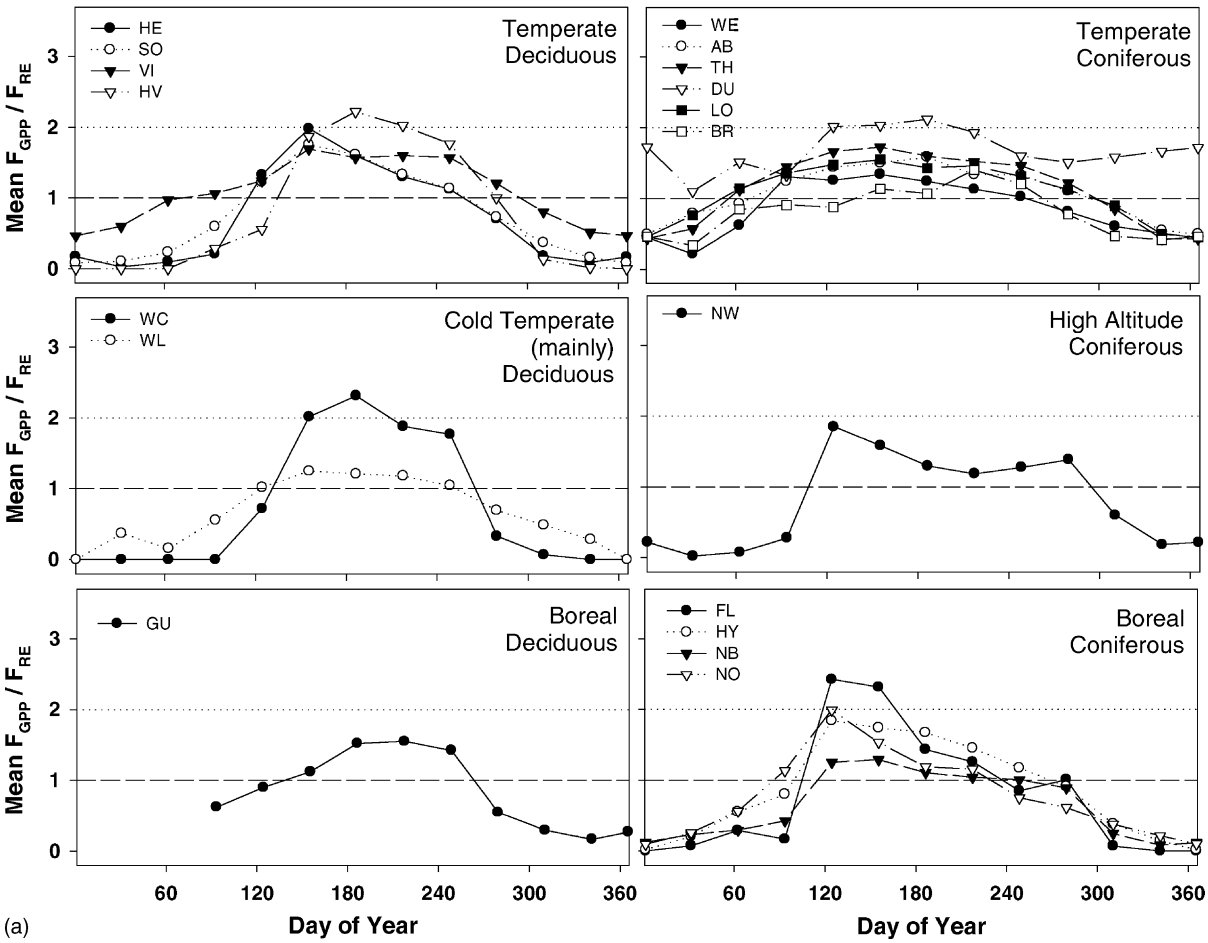

Fig. 8. Seasonal development of the ratio between F_{GPP} and F_{RE} for selected sites from Table 1. (a) Left panels: temperate, cold temperate, and boreal deciduous forests, right panels: temperate, high altitude, and boreal coniferous forests; (b) Maritime coniferous, Mediterranean Broadleaf, rainforest and grasslands. The z-value of 1 (dashed lines) indicates that F_{NEE} equals 0. The z-value of 2 (dotted lines) corresponds to F_{NEE} equals F_{RE}, indicating low overall contribution of F_{RH}.

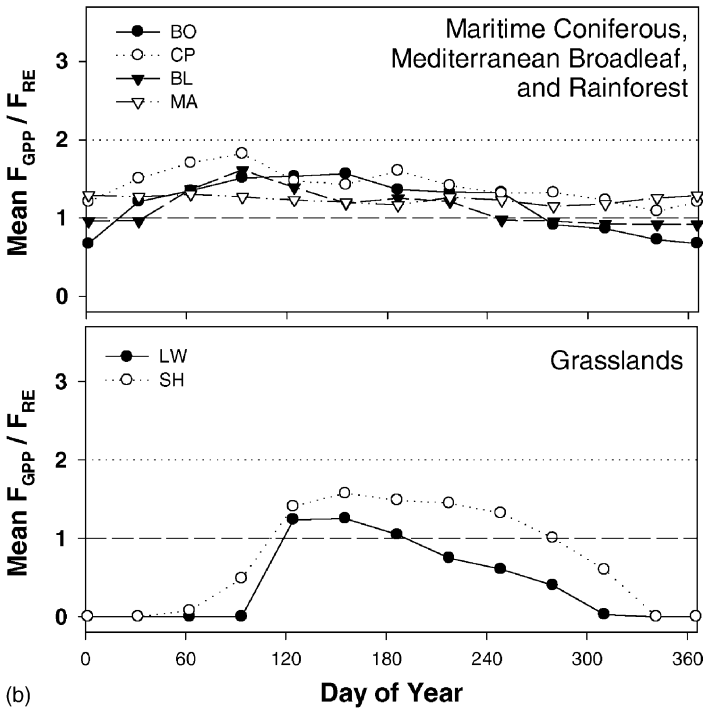

Fig. 8. (*Continued*).

Table 3
Annual sum of F_{GPP} and F_{NEP} estimates of the length of the carbon uptake period, and values of F_{GPP} and F_{NEP} adjusted for season length (F^{d}_{GPP} and F^{d}_{NEP}) for 35 sites from the EUROFLUX and AmeriFlux projects[a]

Site	F_{GPP} (g C m^{-2} per year)	F_{NEP} (g C m^{-2} per year)	$S_{GPP/RE}$ (days)	S_{NEP} (days)	F^{d}_{GPP} (g C m^{-2} per day)	F^{d}_{NEP} (g C m^{-2} per day)
Temperate coniferous forests						
Aberfeldy[b]	1924	597	289	307	6.27	1.95
WeidenBrunnen[b]	1319	−9	146	164	8.04	−0.06
Tharandt[b]	1806	628	257	266	6.79	2.36
Loobos[b]	1394	254	212	213	6.54	1.19
Brasschaat[b]	992	−146	136	173	5.74	−0.84
Wind River[c]	NA	327	NA	365	NA	0.90
Metolius[c]	1570	273	292	365	4.30	0.75
Duke Forest[c]	1487	595	318	339	4.39	1.75
High altitude coniferous forests						
Niwot Ridge[c]	831	71	180	189	4.40	0.38
Boreal coniferous forests						
North Boreas[c]	812	6	142	164	4.95	0.04
Flakaliden[b]	723	115	135	167	4.33	0.69
Norunda[b]	1691	−11	144	142	11.91	−0.08
Hyytiala[b]	959	246	173	182	5.27	1.35
Howland[c]	909	251	195	232	3.92	1.08

Table 3 (*Continued*)

Site	F_{GPP} (g C m^{-2} per year)	F_{NEP} (g C m^{-2} per year)	$S_{GPP/RE}$ (days)	S_{NEP} (days)	F^{d}_{GPP} (g C m^{-2} per day)	F^{d}_{NEP} (g C m^{-2} per day)
Temperate deciduous forests						
Vielsalm[b]	1507	435	218	261	5.77	1.67
Soroe[b]	1276	91	139	141	9.05	0.64
Hesse[b]	1258	129	146	148	8.50	0.87
WalkerBranch[c]	1473	757	216	197	7.48	3.84
Harvard[c]	1122	181	142	138	8.13	1.31
Cold temperate deciduous forests						
Willow Creek[c]	1165	313	134	138	8.44	2.26
Park Falls/WLEF[c]	903	−22	109	136	6.64	−0.16
Boreal deciduous forests						
Gunnarsholt[b]	NA	NA	NA	108	NA	NA
Maritime/Mediterranean evergreen forests						
Bordeaux[b]	1681	454	255	300	5.60	1.51
Castelporziano[b]	1683	585	325	324	5.19	1.81
Sky Oaks young [c]	387	60	174	183	2.11	0.33
Sky Oaks old [c]	734	67	144	168	4.37	0.40
Blodgett Forest[c]	1386	339	256	272	5.10	1.24
Rainforest						
Manaus[c]	3249	608	365	365	8.90	1.66
Grasslands						
LittleWashita[c]	542	−212	65	86	6.30	−2.46
Shidler[c]	1715	362	154	160	10.72	2.26
Risoe[b]	NA	538	NA	253	NA	2.13
Crops						
Bondville[c] C4	1471	588	140	188	7.82	3.13
Bondville[c] C3	599	−115	85	90	6.66	−1.27
Ponca[c]	1396	155	176	211	6.62	0.74
Soroe[b]	1101	303	163	146	7.54	2.08

[a] EUROFLUX projects.

[b] The F_{NEP} based season length (S_{NEP}) is number of days between spring and fall sign change of F_{NEP} (for crops uptake-period of inter-crops is included). $S_{GPP/RE}$ is the length of the period, where $z = F_{GPP}/F_{RE}$ was greater than 1. Values of F^{d}_{GPP} and F^{d}_{NEP} are calculated based on S_{NEP}. Data are averaged for all available years.

[c] AmeriFlux projects.

when F_{RE} is underestimated (e.g., due to problems in nocturnal flux measurements, see below). Generally, values of F_{GPP}/F_{RE} as derived from eddy covariance measurements are high in comparison with model estimates of ecosystem metabolism, for example, seven of eight terrestrial biosphere models evaluated by Nemry et al. (1999) assume or calculate annual equilibrium between F_{RH} and F_{NPP} (or $z = 1$) for all locations. Values of z above 1 could be symptomatic for eddy covariance measurements, because of known uncertainties, especially concerning night-time fluxes or flux measurements in complex terrain (e.g., Lee, 1998; Baldocchi et al., 2000; Aubinet et al., 2000). But they are supported by other evidence pointing to a large northern hemispheric terrestrial carbon sink (e.g., Tans et al., 1990; Friedlingstein et al., 1995; Keeling et al., 1996b; Fan et al., 1998; Ciais et al., 1999).

In principle, an estimate of the photosynthetically active season could be derived from the numbers of days where F_{GPP} is larger than 0. However, the uncertainty of F_{RE} estimates is relatively large, eventually leading to positive F_{GPP} during dormant seasons, as F_{GPP} is calculated as the sum of F_{NEP} and F_{RE}. Therefore the length of the season was determined by (1)

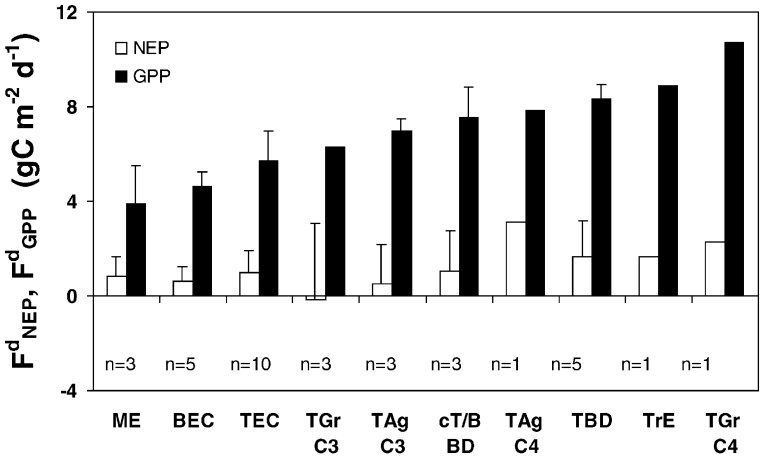

Fig. 9. F_{GPP} and F_{NEP} adjusted for length of the carbon uptake period, and averaged for functional vegetation types (ME: Mediterranean evergreen systems; BEC: boreal evergreen conifers; TrE: rainforest; TGr C3: temperate C_3 grasslands; TAg C3: temperate C_3 crops; TEC: temperate evergreen conifers; TAg C4: temperate C_4 crops; TBD: temperate broad-leaf deciduous; TGr C4: temperate C_4 grasslands. Vertical bars indicate standard deviation of the mean.

calculating the time span between spring and fall sign change in F_{NEE}, and (2) by counting all days where $F_{GPP}/F_{RE} > 1$, i.e., F_{NEP} is positive (Table 3, S_{NEP} and $S_{GPP/RE}$, respectively). Annual sums of F_{GPP} and F_{NEP} were divided by S_{NEP} to determine F^d_{GPP} and F^d_{NEP}, values of F_{GPP} and F_{NEP} adjusted for the length of the season. A comparison of these numbers averaged for functional or biome type is given in Fig. 9. Similar values were found for F^d_{GPP} at the C_4 crop systems and temperate and cold temperate/boreal deciduous forest sites (7.8, 8.3 and 7.5 g C m^{-2} per day), for the temperate conifers, C_3 crops and C_3 grasslands (5.7, 6.9 and 6.3 g C m^{-2} per day, respectively), and the boreal conifers (4.6 g C m^{-2} per day). Values for the Mediterranean systems and a C_4 grassland were 3.9 and 10.7 g C m^{-2} per day, the rate at the tropical site was 8.9 g C m^{-2} per day. The patterns observed for F^d_{GPP} were not reproduced in patterns in F^d_{NEP} which decreased from 3.1 to −0.2 g C m^{-2} per day in the order C_4 crops > C_4 grasslands > temperate deciduous forests, and rainforest > cold temperate/boreal deciduous forests > temperate conifers > Mediterranean systems > boreal conifers > C_3 crops > C_3 grasslands. The results for the grasslands might be biased due severe drought in one C_3 system, and the fact that the C-loss during prescribed burning in the C_4 system is not included in the data. In general, F^d_{NEP} is positive indicating nearly all of the ecosystems in this study represent net sinks for atmospheric CO_2. These tower-based estimates need to be confirmed by other methods, for example based on careful allometry. Nevertheless, the overall observed patterns are reasonable, for instance the C_4 systems showing higher carbon uptake than the C_3 systems, or the relative consistency within the temperate C_3 systems (with the exception of temperate deciduous forest sites).

Eddy covariance data do not provide values of F_{NPP} (net primary productivity $= F_{NEP} + F_{RH}$), and there are no direct methods to estimate F_{NPP} from F_{NEP} or F_{GPP}. Separate measurements of F_{RH} would be needed. However, F_{NPP} is the traditional measure of plant productivity in forestry and agriculture and extensive data sets are available. More recently measurements of F_{NPP} have been used to parameterize and evaluate models of terrestrial carbon cycling to assess the impacts of global land-use and climate change (e.g., Cramer et al., 1999; Jiang et al., 1999; Nemry et al., 1999), and for validation of remote sensing data (Field et al., 1995; Goetz et al., 1999; Running et al., 1999). We used three different sources of F_{NPP} data of various vegetation types (Lieth, 1975; Schulze, 1982; Waring and Schlesinger, 1985) for comparison with annual F_{NEP} and F_{GPP} derived from eddy covariance measurements (Fig. 10). A ratio of 0.45 was used to convert biomass dry weight to carbon content, if

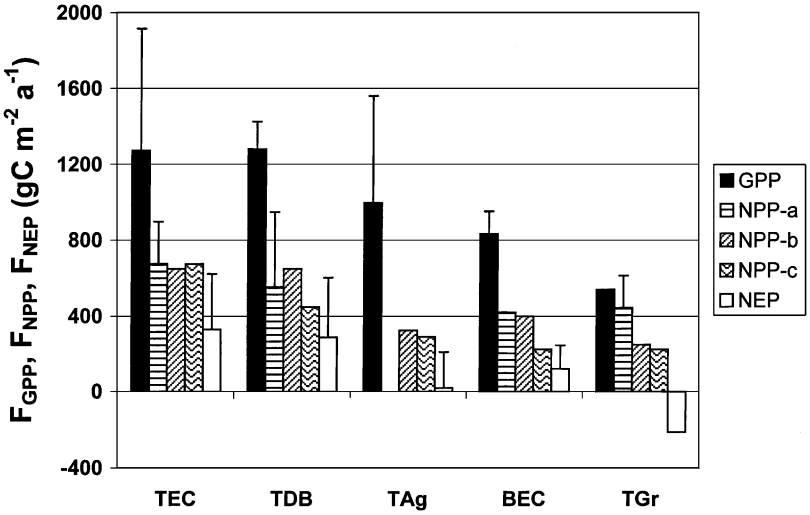

Fig. 10. Average F_{GPP}, F_{NPP} and F_{NEP} for different vegetation types: TEC, temperate evergreen conifers; TDB, temperate deciduous broad-leaf forest; Tag, temperate crops; BEC, boreal evergreen conifers; TGr, temperate grasslands. Vertical bars indicate standard deviation of the mean. F_{GPP}, and F_{NEP} are derived from the eddy covariance data of this study. The three F_{NPP} estimates are from (a) Schulze (1982), (b) Waring and Schlesinger (1985), and (c) Lieth (1975).

applicable. For the forest ecosystems annual F_{GPP}, F_{NPP} and F_{NEP} all decreased comparing the temperate and boreal zones. However, the decrease in F_{NEP} is greater than in F_{NPP} or F_{GPP}. Our results show a strong latitudinal trend in the ratio F_{NEP}/F_{GPP} for forest ecosystems: 26% for the temperate evergreen conifers, 23% for the temperate deciduous broad-leaf forests, and 15% for the boreal evergreen conifers. The relative contribution of F_{NPP} to F_{GPP} is more constant: 51% for the temperate evergreen conifers and temperate deciduous broad-leaf forests, and 48% for the boreal evergreen conifers. These values highlight a similar contribution of autotrophic respiration to ecosystem carbon metabolism in the temperate and the boreal systems (49–52%). On the other hand, total respiratory costs of assimilated carbon are higher in the boreal systems (85% for boreal systems compared to 74–77% for temperate), indicating a larger contribution of F_{RH} to total ecosystem respiration in boreal systems.

5. Conclusion

Using tower-base ecosystem-atmosphere exchange data from the FLUXNET database, we have investigated seasonal patterns of F_{GPP}, and F_{RE}, derived values of F_{NEE} and F_{GPP} adjusted for length of the carbon uptake period and compared annual F_{GPP} with F_{NPP} from inventory studies for sites from a series of functional vegetation types. The analysis included boreal and temperate, deciduous and coniferous forests, Mediterranean evergreen systems, a rainforest, temperate grasslands, and C_3 and C_4 crops.

Striking parallels in the seasonal pattern of F_{GPP} and F_{RE} were observed within and between the vegetation types, in terms of seasonal amplitude and phasing of net carbon fluxes, and the relative contribution of photosynthesis and respiration. Our results indicate that temperate and boreal conifers should be viewed as separate classes. Generalized seasonal patterns might be utilized by global modelers and in inversion studies, and to validate the phenology modules of plot scale models.

For the temperate deciduous and boreal conifers, we identified periods of unbalanced respiratory and assimilatory processes, indicating a potentially higher susceptibility to changes in management practices or climatic conditions, especially considering the expected larger increase in night-time temperatures globally, and greater temperature increases at high latitudes.

Table 4
Minimum, maximum, average and standard deviation of regression coefficients R^2 of 32 sites from the EUROFLUX and AmeriFlux projects

Site	Year	R^2				Periods (n)
		Minimum	Maximum	Average	S.D.	
Temperate coniferous forests						
Aberfeldy[a]	1998	0.793	0.97	0.902	0.049	335
WeidenBrunnen[a]	1998	0.539	0.969	0.871	0.105	317
Tharandt[a]	1999	0.336	0.864	0.696	0.164	335
Loobos[a]	1997	0.12	0.89	0.721	0.127	322
Brasschaat[a]	1998	0.22	0.845	0.683	0.14	321
Wind River[b]	1998	0.12	0.615	0.373	0.16	223
Howland[b]	1997	0.102	0.705	0.493	0.174	335
Duke Forest[b]	1999	0.288	1	0.604	0.162	305
High altitude coniferous forests						
Niwot Ridge[b]	2000	0.543	0.977	0.809	0.127	335
Boreal coniferous forests						
North Boreas[b]	1995	0.162	0.926	0.682	0.239	335
Flakaliden[a]	1997	0.16	0.86	0.717	0.138	330
Norunda[a]	1997	0.221	0.818	0.645	0.138	335
Hyytiala[a]	1998	0.206	0.975	0.751	0.248	335
Temperate deciduous forests						
Vielsalm[a]	1998	0.131	0.596	0.382	0.109	335
Soroe[a]	1997	0.246	0.952	0.686	0.216	335
Hesse[a]	1998	0.461	0.871	0.718	0.1	335
Harvard[b]	1999	0.441	0.902	0.774	0.092	335
WalkerBranch[b]	1998	0.123	0.67	0.445	0.157	335
Cold temperate deciduous forests						
Park Falls/WLEF	1998	0.173	0.873	0.587	0.182	335
Willow Creek[b]	2000	0.29	0.841	0.685	0.125	335
Boreal deciduous forests						
Gunnarsholt[a]	1997	0.277	0.978	0.805	0.173	263
Maritime/Mediterranean evergreen forests						
Bordeaux[a]	1998	0.885	0.992	0.947	0.03	181
Castelporziano[a]	1997	0.614	0.773	0.704	0.032	335
Sky Oaks young [b]	1998	0.607	0.999	0.832	0.092	207
Sky Oaks old [b]	1998	0.91	1	0.966	0.023	101
Blodgett Forest[b]	2000	0.642	0.999	0.85	0.066	152
Grasslands						
LittleWashita[b]	1998	0.053	0.897	0.6	0.224	289
Shidler[b]	1997	0.306	0.973	0.824	0.2	335
Crops						
Bondville[b]	2000	0.051	0.964	0.574	0.288	332
Bondville[b]	1997	0.057	0.874	0.49	0.291	305
Ponca[b]	1997	0.781	0.979	0.894	0.042	229
Soroe[a]	1999	0.101	0.761	0.466	0.147	280

[a] EUROFLUX projects.
[b] AmeriFlux projects.

Overall, most of the sites we investigated sequester carbon, supporting the widely reported northern hemispheric terrestrial biosphere sink.

Our observation that F^{d}_{GPP}, adjusted for the length of the season, is not constant over various functional vegetation types and has important validation potential for global carbon cycle modeling. For the sites in this study, values of F^{d}_{GPP} decreased from 10.7 to 2.4 g C m^{-2} per day in the order C_4 grassland > rainforest > C_4 crops and temperate deciduous forests > C_3 crops, grassland and temperate conifers > boreal conifers > Mediterranean systems.

To investigate the impacts of global land-use and climate change, models of terrestrial carbon cycling and validation approaches of remote sensing data primarily assess F_{NPP}. Comparing F_{NPP} from various literature sources with annual values of F_{NEP} and F_{GPP} well-known latitudinal gradients were confirmed, and the relative contribution of F_{RH} to the total respiratory costs of assimilation of various vegetation types was estimated. However, our ability to compare our results directly to on-site estimates of F_{NPP} is constrained by the lack of sites where both long-term eddy covariance data and measurements of net primary productivity are available. To overcome these limitations future investigations at tower sites should preferably be complemented by inventory studies of carbon stock changes.

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Appendix A

Estimates of F_{GPP} depend crucially on the quality of derived F_{RE} values, as F_{GPP} is calculated as the sum of F_{RE} and measured F_{NEP}. Apparently, the derivation of F_{RE} and the quality of the fit of Eq. (1) to night-time fluxes of F_{NEP} is critical to all the results and conclusions presented in this paper. During data processing ca. 36,000 of such fits were performed, 335 fits for each of 103 site-years (335 running periods of 30-days; for more information, see Section 2). For illustration, Table 4 lists minimum, maximum, average and standard deviation (S.D.) of the 335 R^2-values of one-third of the available site-years. Comparing the average R^2 and S.D. of all 103 site-years reveals that maritime/Mediterranean systems and coniferous forests show the largest average ($R^2 = 0.73$ and 0.72). Deciduous forests and grasslands have intermediate values of average $R^2 = 0.65$ and 0.70, respectively. Lowest average R^2 of 0.61 are found for the cropland sites, indicating that the confidence in derived F_{RE} values decreases in the order evergreen forest > deciduous forest > grassland > crop sites. In addition, the seasonal variation in R^2 increases in more or less the same order, indicated by the average standard deviation of F_{RE} values within those groups, 0.08 for the maritime/Mediterranean sites, 0.14 for coniferous forest sites, 0.15 for deciduous forest sites, 0.23 for grasslands, and 0.22 for crops. Especially for the latter the seasonal values of R^2 were quite variable: periods where R^2 dropped below 0.2 coincided, e.g. with non-vegetated periods for crops, or temperatures below freezing. Yet during those periods overall respiration rates are expected to be quite low, so that eventual errors due to the low quality of the fit are small, and we decided to keep the respective F_{RE} estimates to calculate monthly and annual sums of F_{RE} and F_{GPP}.

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