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Soil respiration at mean annual temperature predicts annual total across vegetation types and biomes

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Abstract. Soil respiration (SR) constitutes the largest flux of CO₂ from terrestrial ecosystems to the atmosphere. However, there still exist considerable uncertainties as to its actual magnitude, as well as its spatial and interannual variability. Based on a reanalysis and synthesis of 80 site-years for 57 forests, plantations, savannas, shrublands and grasslands from boreal to tropical climates we present evidence that total annual SR is closely related to SR at mean annual soil temperature (SR_{MAT}), irrespective of the type of ecosystem and biome. This is theoretically expected for non water-limited ecosystems within most of the globally occurring range of annual temperature variability and sensitivity (Q_{10}). We further show that for seasonally dry sites where annual precipitation (P) is lower than potential evapotranspiration (PET), annual SR can be predicted from wet season

SR_{MAT} corrected for a factor related to P/PET . Our finding indicates that it can be sufficient to measure SR_{MAT} for obtaining a well constrained estimate of its annual total. This should substantially increase our capacity for assessing the spatial distribution of soil CO₂ emissions across ecosystems, landscapes and regions, and thereby contribute to improving the spatial resolution of a major component of the global carbon cycle.

1 Introduction

In view of its implications for the climate system, the carbon (C) cycle has received increasing attention over the recent years (Denman et al., 2007). Recent global estimates suggest that soils emit about 98 Pg C per year, which exceeds emission rates from fossil fuel combustion by an order of magnitude (Bond-Lamberty and Thomson, 2010; Denman et al., 2007). While indicating that soils are the



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predominant source of CO₂ from terrestrial ecosystems, such estimates are still highly uncertain. They are based on a highly restricted dataset, which heavily underrepresents not only many biomes, but also the considerable spatial and temporal variability of SR within any given biome. Recently, progress has been made in illuminating factors determining the diurnal, seasonal and interannual variability of SR within ecosystems (Bahn et al., 2010; Davidson et al., 2006a; Vargas et al., 2010). At the same time we still lack tools permitting a rapid assessment of the spatial variability of SR across ecosystems, landscapes and regions – which would be essential for deriving more defensible regional and global estimates of SR.

It is evident that, even within short distance, similar types of ecosystems may exhibit substantial differences in annual SR (Bahn et al., 2008; Curiel Yuste et al., 2004; Kang et al., 2003; Vincent et al., 2006). Spatial assessments of total annual SR (SR_{annual}) are difficult to achieve given a finite availability of resources and the resulting trade-off between the temporal resolution required for obtaining an annual estimate and the spatial coverage required for achieving a defensible regional up-scaling (Savage and Davidson, 2003). For this reason it has been attempted to identify proxies for estimating SR_{annual}, including monthly air temperature and precipitation (Raich and Potter, 1995; Raich et al., 2002), litterfall (Davidson et al., 2002; Raich and Nadelhoffer, 1989) and productivity indices, such as leaf area index or gross primary productivity (Bahn et al., 2008; Hibbard et al., 2005; Janssens et al., 2001; Reichstein et al., 2003).

Here, we demonstrate that SR measured at mean annual temperature (SR_{MAT}) may be a useful and meaningful predictor of SR_{annual}. We do so by first outlining a theoretical framework, suggesting that SR_{MAT} is in principle well suited for estimating SR_{annual} at non water-limited sites within most of the globally occurring range of annual soil temperature variability and temperature sensitivity of SR (Q_{10}). Secondly, we apply a Monte-Carlo analysis to test the hypothesized relationship between SR_{MAT} and SR_{annual} on a randomly generated dataset. Thirdly, we explore the relationship for existing databases of SR for 57 forests, plantations, savannas, shrublands and grasslands from boreal to tropical climates. We show that for seasonally dry ecosystems, where mean annual temperature occurs only in the wet season, SR_{annual} can be estimated from wet season SR_{MAT} and a correction factor based on the ratio of precipitation to potential evapotranspiration. Finally, based on additional 23 site-years for four temperate forests, we analyse effects of inter-annual variability on estimates of SR_{annual}. Our finding indicates that it is sufficient to measure SR_{MAT} for obtaining a highly constrained estimate of its annual total, which could help improving future assessments of the spatial distribution of soil CO₂ emissions across ecosystems, landscapes and regions.

2 Methods

2.1 Annual soil temperature variability across biomes

A global overview of the annual variability of soil temperature, expressed as the standard deviation of daily means of soil temperature (T_{sd}), was obtained from the FLUXNET data set (<http://www.fluxdata.org/default.aspx>) and included all sites reporting continuous quality-controlled data for soil temperature which were made available by the site principal investigators. In total 172 sites and 474 site-years were included in the analysis. Sites were grouped to the following climatic zones: tropical (7 sites), dry (6 sites), subtropical-mediterranean (47 sites), temperate (49 sites), temperate continental (35 sites), boreal (24 sites) and arctic climates (4 sites). For sites reporting multiple years of soil temperature an average T_{sd} of all reported years was used.

2.2 Soil respiration database

The soil respiration database consisted of 35 sites and 58 site-years for temperate and boreal forests and grasslands, 7 tropical forests and plantations, and 15 mediterranean, dry sub-humid and semi-arid forests, savannas, grasslands and shrublands, as summarized in Table 1. The database also includes 11 previously unpublished datasets, which were obtained using a range of closed and open dynamic soil respiration systems on previously installed shallow collars. All these systems are well established systems that are either commercially available (Licor, Lincoln, Nebraska, USA) or have been tested and described in further detail in previous studies (Rayment and Jarvis, 1997; Carbone et al., 2008). Measurements were taken either manually in bi-weekly to monthly intervals or continuously, using automated soil respiration systems. Details on the systems used at the respective sites, and on sampling frequencies and spatial replication are provided in Table 2. In parallel to soil respiration measurements, soil temperature (using soil temperature probes) and soil moisture (using TDR probes) were recorded mostly in 5 cm depth.

SR_{MAT}, i.e. the rates of soil respiration occurring at mean annual soil temperature, for all sites and years were calculated using the soil temperature – respiration response functions reported by the respective studies. The average annual temperature sensitivity of SR, expressed as Q_{10} , has been listed for all sites in Table 1. For some tropical sites with minor seasonal differences in soil temperature and for several seasonally dry ecosystems no well constrained or meaningful (cf. e.g. Davidson et al., 2006) Q_{10} value could be provided. Calculated SR_{MAT} was cross-checked against SR values actually measured at MAT. The annual variability of soil temperature (T_{sd}) was calculated from the original data records as the standard deviation of daily means of soil temperature for the reported years.

Table 1. Vegetation type, location, mean and standard deviation of annual soil temperature (as based on daily means), mean annual precipitation (MAP), ratio of precipitation/potential evapotranspiration (P/PET), as extracted from a global grid model, Q_{10} of soil respiration, soil respiration at mean annual temperature (SR_{MAT} – wet season values are set in italics) and annual soil respiration (SR_{annual}) for the sites included in this study. Sources: 1...Bahn et al., 2008; 2...Janssens et al., 2001 and 2003; 3...Curiel Yuste et al., 2004; 4...Janssens and Pilegaard, 2003; 5...Savage et al., 2009; 6...Davidson et al. 2006c, and some additional unpublished data from Savage and Davidson; 7...Davidson et al., 2006b, and some additional unpublished data from Savage and Davidson; 8...Roupsard and Epron, unpublished; 9...Salimon et al., 2004; 10...Davidson et al., 2008; 11...Davidson et al., 2000; 12...Nouvellon and Epron, unpublished; 13...Nouvellon and Epron, unpublished; 14...Misson, unpublished; 15...Gimeno et al., unpublished; 16...Tang and Baldocchi, 2005; 17...Wieser et al., 2009; 18...Carbone and Trumbore, unpublished; 19...Vargas and Allen, 2008; 20...Grünzweig et al., 2009; 21...Talmon and Grünzweig, unpublished.

Site	Vegetation	Location	MAT (s.d.) (°C)	MAP (mm)	P/PET (–)	Q_{10} (–)	SR_{MAT} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	SR_{annual} ($\text{g C m}^{-2} \text{ y}^{-1}$)	Ref
<i>Boreal and temperate grasslands and forests</i>									
Amplero	Grassland	41°54' N 13°36' E	11.7 (8.5)	1365	1.12	2.0	4.25	1305	1
Monte Bondone	Grassland	46°02' N 11°07' E	9.6 (8.2)	1189	1.82	3.4	5.39	1743	1
Oensingen	Grassland	47°17' N 7°44' E	10.8 (8.1)	1200	2.20	2.3	4.05	1988	1
Stubai 1	Grassland	47°17' N 11°32' E	9.0 (8.2)	850	2.20	2.2	3.70	1792	1
Stubai 3	Grassland	47°17' N 11°32' E	6.9 (6.8)	1097	2.52	2.6	1.51	729	1
Berchtesgaden 1	Grassland	47°37' N 12°35' E	8.0 (6.5)	1665	2.52	2.7	3.14	1378	1
Berchtesgaden 2	Grassland	47°37' N 12°35' E	6.9 (6.2)	1665	2.52	2.3	2.18	907	1
Berchtesgaden 3	Grassland	47°37' N 12°35' E	7.6 (6.4)	1665	1.59	2.5	2.50	1070	1
Carlow	Grassland	52°85' N 6°54' E	10.2 (4.4)	974	1.61	2.4	3.19	1153	1
AuchencorthMoss	Grassland	55°79' N 3°24' E	6.9 (3.3)	970	1.89	5.7	1.20	529	1
Cow Park	Grassland	55°52' N 3°12' E	8.9 (4.9)	849	1.46	2.1	4.33	1246	1
Varriö	Grassland	67°72' N 29°60' E	3.3 (5.4)	500	1.12	2.2	0.13	58	1
IT 1	<i>Fagus sylvatica</i> forest	41°52' N 13°38' E	2.5 (–)	1100	1.12	2.2	2.27	879	2
ITex	<i>Picea abies</i> , <i>Pinus cembra</i> forest	46°35' N 11°26' E	4.0 (6.1)	1010	1.58	3.4	2.35	1379	2
BE1Douglas	<i>Fagus sylvatica</i> , <i>Pseudotsuga</i> forest	50°18' N 6°00' E	8.1 (4.8)	1000	1.53	3.0	1.14	430	2
BE1beech	<i>Fagus sylvatica</i> , <i>Pseudotsuga</i> forest	50°18' N 6°00' E	8.1 (4.8)	1000	1.53	2.4	2.20	844	2
FR1 – mean 1996–1998	<i>Fagus sylvatica</i> forest	48°40' N 7°05' E	9.4 (4.7)	820	1.32	4.0	1.72	636	2
1996							1.43	509	2
1997							1.71	685	2
1998							2.02	713	2
DK – mean 1996–1998	<i>Fagus sylvatica</i> forest	56°00' N 12°20' E	7.4 (4.6)	600	1.18	5.0	0.97	473	2
1996							0.60	370	2
1996							1.18	460	2
1998							1.12	590	2
GE1-47y	<i>Picea abies</i> forest	50°09' N 11°52' E	6.1 (–)	890	1.36	2.4	1.71	709	2
GE1-87y	<i>Picea abies</i> forest	50°09' N 11°52' E	6.1 (–)	890	1.36	3.2	1.65	740	2
GE1-111y	<i>Picea abies</i> forest	50°09' N 11°52' E	6.1 (–)	890	1.36	2.9	1.98	859	2
GE1-146y	<i>Picea abies</i> forest	50°09' N 11°52' E	6.1 (–)	890	1.36	2.4	1.49	624	2
GE-Kiel	<i>Fagus sylvatica</i> forest	54°06' N 10°14' E	7.6 (–)	697	1.56	3.9	1.15	590	2
SE1	<i>Picea abies</i> , <i>Pinus sylvestris</i> forest	60°05' N 17°28' E	5.7 (4.4)	530	1.14	2.8	2.18	1080	2
Bra2001A	<i>Pinus sylvestris</i> , <i>Quercus robur</i> forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	1.9	1.16	458	3
Bra2001B	<i>Pinus sylvestris</i> , <i>Quercus robur</i> forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	1.9	1.57	560	3
Bra2001C	<i>Pinus sylvestris</i> , <i>Quercus robur</i> forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	2.4	1.39	492	3
Bra2001D	<i>Pinus sylvestris</i> , <i>Quercus robur</i> forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	3.3	2.18	935	3
Bra2001E	<i>Pinus sylvestris</i> , <i>Quercus robur</i> forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	4.8	1.71	674	3
Bra2001F	<i>Pinus sylvestris</i> , <i>Quercus robur</i> forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	2.5	2.43	893	3
DK1	<i>Fagus sylvatica</i> forest	55°29' N 11°38' E	8.0 (4.4)	600	1.18	4.0	1.38	605	4
DK2	<i>Fagus sylvatica</i> forest	56°00' N 12°20' E	8.0 (4.4)	600	1.18	4.6	1.21	583	4
DK3	<i>Fagus sylvatica</i> forest	56°00' N 12°20' E	8.0 (4.4)	600	1.18	4.1	1.29	515	4
Harvard Forest - 2003 (automated SR chambers)	Mixed hardwood forest	42°32' N 72°11' W	9.8 (6.5)	1089	1.14	3.8	2.09	860	5
<i>Interannual – manual SR chambers – 1997</i>									
1998			7.1 (6.5)	908		3.9	1.73	626	6
1999			8.5 (6.4)	954		6.3	1.89	992	6
2000			8.7 (6.5)	1034		3.2	1.16	450	6
2001			8.0 (6.0)	1061		4.9	2.46	959	6
			8.4 (6.4)	808		2.1	2.37	793	6

Table 1. Continued.

Site	Vegetation	Location	MAT (s.d.) (°C)	MAP (mm)	P/PET (–)	Q ₁₀ (–)	SR _{MAT} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	SR _{annual} ($\text{g C m}^{-2} \text{ y}^{-1}$)	Ref
2002	V	8.6 (6.3)	7.0 (6.3)	1111	4.4	3.5	2.43	979	6
2003			1310	2.41		958	6		
2004			7.5 (6.9)	1163		5.2	2.26	926	6
2005			8.5 (7.2)	1426		4.3	1.83	893	6
2006			8.9 (6.3)	1095		3.8	1.72	796	6
2007			8.9 (8.4)	1139		4.8	1.64	825	6
2008			9.1 (6.3)	1565		2.4	2.37	921	6
Howland – 2005	Mixed evergreen forest (automated chambers)	45°12' N 68°44' W	6.5 (6.4)	1005	1.27	3.4	1.64	750	5
Interannual – manual SR chambers – 2000			6.1 (6.1)	767		4.5	2.20	747	7
2001			7.8 (5.6)	524		2.9	2.47	754	7
2002			7.8 (6.2)	798		2.7	2.30	701	7
2003			7.1 (6.9)	952		3.2	2.59	857	7
2004			7.0 (6.4)	763		3.7	2.61	752	7
2005			7.1 (6.9)	1280		4.0	2.50	788	7
2006			6.9 (7.1)	1105		3.5	2.78	823	7
2007			6.7 (6.5)	723		3.2	2.36	679	7
2008			7.7 (6.1)	810		3.0	2.85	862	7
Tropical forests and plantations									
Vanuatu	Coco plantation	15°27' S 167°12' E	26.6 (1.4)	2760	2.60	1.0	5.00	1917	8
Rio Branco	Rainforest	9°56' S 67°52' W	23.8 (0.8)	1940	1.24	5.6	4.73	1620	9
Tapajos	Rainforest	2°90' S 54°95' W	26.0 (–)	2090	1.50	–	3.38	1279	10
Paragominas	Primary forest	2°59' S 47°31' W	23.0 (0.7)	1784	1.50	1.0	5.24	2000	11
Itatinga	Eucalytus plantation	23°01' S 48°32' W	19.1 (2.0)	1360	1.01	–	3.13	1071	12
Kondi	Eucalytus plantation, 5 y	4°35' S 11°75' E	25.8 (2.0)	1400	1.27	–	1.31	465	13
Kondi	Eucalytus plantation, 13 y	4°35' S 11°75' E	25.8 (2.0)	1400	1.27	–	2.13	744	13
Mediterranean, subhumid and semiarid forests, savannas, shrublands and grasslands									
Puechabon	Quercus forest	43.7414 N 3.59583 E	12.3 (5.4)	844	1.00	1.9	2.73	762	14
Alinya	Grassland	42°12' N 1°27' E	8.5 (7.8)	700	0.81	2.1	1.99	494	1
IT2	Quercus ilex forest	41°45' N 12°22' E	14.5 (5.5)	770	0.73	2.0	5.87	1456	2
Las Majadas del Tietar	Quercus ilex savanna	39°56' N 5°46' W	19.2 (10.1)	528	0.64	2.5	3.08	683	15
Savanna grassland open	Savanna grass	38°43' N 120°96' W	17.7 (6.9)	496	0.46	1.1	1.60	394	16
Savanna trees	Quercus douglasii	38°43' N 120°96' W	17.7 (6.9)	496	0.46	1.2	2.15	616	16
Tenerife	Pinus canariensis forest	28°35' N 27°15' W	10.4 (–)	460	0.45	3.9	2.50	726	17
James Reserve forest	Quercus/Pinus forest	33°48' N 116°46' W	9.0 (6.6)	507	0.30	–	4.05	892	18
James Reserve woody	Quercus/Pinus forest	33°48' N 116°46' W	11.8 (6.7)	507	0.30	1.7	1.9	764	19
James Reserve herb.	Eriogonum wrightii	33°48' N 116°46' W	10.8 (7.9)	507	0.30	1.7	1.25	524	19
Yatir forest	Pinus halepensis forest	31°20' N 35°03' E	20.7 (7.9)	280	0.19	1.2–2.5	2.68	458	20
Semi-arid shrubland	Sarcopoterium spinosum	31°23' N 34°54' E	21.7 (7.6)	300	0.18	1.6	4.22	731	21
Semi-arid shrubland	Intershrub microsite	31°23' N 34°54' E	22.9 (8.9)	300	0.18	1.4	2.25	345	21
Dry subhumid shrubland	Sarcopoterium spinosum	31°42' N 35°03' E	19.1 (6.6)	540	0.32	1.6	3.89	754	21
Dry subhumid shrubland	Intershrub microsite	31°42' N 35°03' E	21.2 (8.2)	540	0.32	1.8	3.87	660	21

2.3 Monte Carlo analysis

Monte Carlo methods are a class of computational algorithms that rely on repeated random sampling to compute their results. Here, we used a Monte Carlo analysis for theoretically testing the hypothesized relationship between SR_{MAT} and SR_{annual} for random combinations of SR_{MAT}, T_{sd} and Q₁₀, constrained to a range of values commonly occurring across the globe (see also Table 1 and Fig. 2). Our analysis was based on 1000 random combinations of SR_{MAT} (range 0–8.0 $\mu\text{mol m}^{-2} \text{ s}^{-1}$), T_{sd} (2–15 °C) and Q₁₀ (1.0–6.0). The variables were generated from independent Gaussian distributions with the following means and standard deviations, which were derived from the available field data: 2.66 (s.d.=0.98) for Q₁₀, 2.89 (1.48) for SR_{MAT}, and 6.7 (1.8) for T_{sd}.

2.4 Aridity index

A generally comparable aridity index for all sites was derived by relating estimates of precipitation (P) to estimates of potential evaporation (PET), which were obtained as follows. Potential evapotranspiration was calculated according to the Modified-Hargreaves method (Droogers and Allen, 2002). This method uses potential radiation (top of atmosphere), average air temperature (2 m), the diurnal temperature range as well as precipitation as predictors. Global monthly grids at 0.5° resolution were calculated and extracted for each site from the grid cell closest to the site. Air temperature grids were derived from CRU (Climate Research Unit) climate data (New et al., 2002), homogenized and extended to 2007 (Österle et al., 2003). Precipitation data were obtained from the GPCC project (Global Precipitation Climatology

Table 2. Methods for measuring soil respiration for previously unpublished datasets. References as in Table 1. CDS and ODS refer to closed and open dynamic system, respectively.

Site (Reference)	System and instrumentation	Replication, sampling frequency
Vanuatu (7)	CDS, Li-6000-09 chamber + Li-6200 (Licor)	64 collars, monthly
Itatinga (11)	CDS, Li8100-103 survey chamber + Li8100 Licor, (Licor)	27 collars (20 cm), bi-weekly
Kondi (12)	CDS, Li8100-102 survey chamber + Li8100 (Licor)	27 collars (10 cm), bi-weekly
Puechabon (13)	ODS (cf. Rayment and Jarvis, 1997)	4–12 chambers, continuous
Las Majadas del Tietar (14)	ODS (cf. Rayment and Jarvis, 1997), Li6262 (Licor)	6 chambers, continuous
James Reserve forest (18)	CDS, as in (Carbone et al., 2008)	8 chambers, continuous
Semi-arid and dry subhumid shrublands (20)	CDS, LI-6400-09 + Li-6400 (Licor)	10 collars, bi-weekly to monthly

Centre; cf. gpcc.dwd.de for documentation). For each location potential evapotranspiration and precipitation were extracted for 27 years (1982–2008) and averaged on a monthly and an annual basis. Extracted mean annual precipitation closely matched the values reported for the sites (Table 1; $\text{MAP}_{\text{predicted}}=1.02 \cdot \text{MAP}_{\text{measured}}$, $R^2=0.88$).

3 Results and discussion

3.1 Theoretical considerations

Major drivers of SR include abiotic (temperature, soil moisture) and biotic (gross primary productivity) factors (Bahn et al., 2009; Davidson et al., 2006a; Trumbore, 2006). Even though differences in SR across sites are largely determined by productivity, both of these fluxes increase with temperature. Therefore soil temperature (T) typically suffices to explain most of the seasonal variation of SR in ecosystems without extended periods of drought (Bahn et al., 2008; Hibbard et al., 2005; Janssens et al., 2001; Reichstein et al., 2003). Thus, $\text{SR}_{\text{annual}}$ of these sites can be estimated from a temperature response function, as based on SR at a reference temperature, the temperature sensitivity of SR (Q_{10} , the factor by which SR is multiplied when the temperature increases by 10°C) and the seasonal course of T . We define the mean annual temperature occurring at any site as the reference temperature, which permits the most generalized testing of our hypothesis across different climates.

Theoretically, if T is constant throughout the year (i.e. its standard deviation is 0), Q_{10} will have no effect on $\text{SR}_{\text{annual}}$. In this case SR at mean annual temperature (SR_{MAT}) scales directly to $\text{SR}_{\text{annual}}$, and their ratio expressed on the same basis (i.e. $\text{mean SR}_{\text{annual}}/\text{SR}_{\text{MAT}}$) equals 1 (Fig. 1). As the seasonal amplitude of temperature (T_{sd} , defined as the standard deviation of daily mean soil temperature over the course

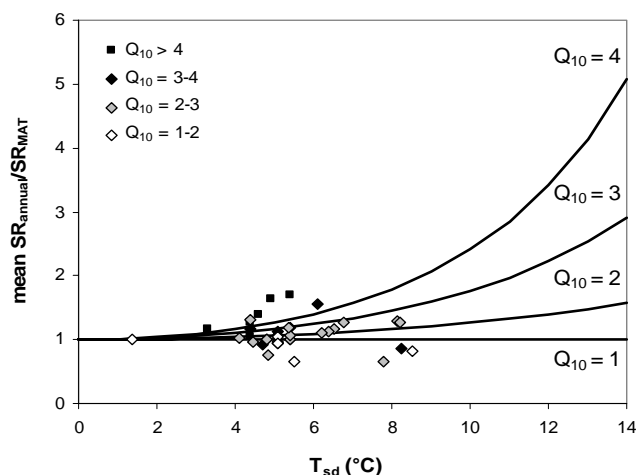


Fig. 1. The ratio of mean annual soil respiration (mean $\text{SR}_{\text{annual}}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$) over soil respiration at mean annual temperature (SR_{MAT} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) as affected by the annual variation of soil temperature (T_{sd}) and Q_{10} of the temperature – soil respiration relationship. Data points indicate values of the non water-limited sites for mean $\text{SR}_{\text{annual}}/\text{SR}_{\text{MAT}}$, T_{sd} and Q_{10} classes.

of the year) increases, Q_{10} becomes increasingly important because the temperature response of SR is not linear. Hence the degree to which Q_{10} affects mean $\text{SR}_{\text{annual}}/\text{SR}_{\text{MAT}}$ increases with increasing T_{sd} (Fig. 1). A recently emerging global dataset of sites (FLUXNET; <http://www.fluxdata.org/default.aspx>; Baldocchi, 2008) indicates that T_{sd} increases from tropical to temperate and continental climates (Fig. 2). The median of T_{sd} was 0.7°C at tropical sites and between 5.5 and 7.4°C in all other climates, 95% of all values being lower than 10.1°C . Exceptionally high values of T_{sd} exceeding 10.5°C occurred in three non-forested ecosystems, two of which were burned open shrubland. Thus T_{sd} normally

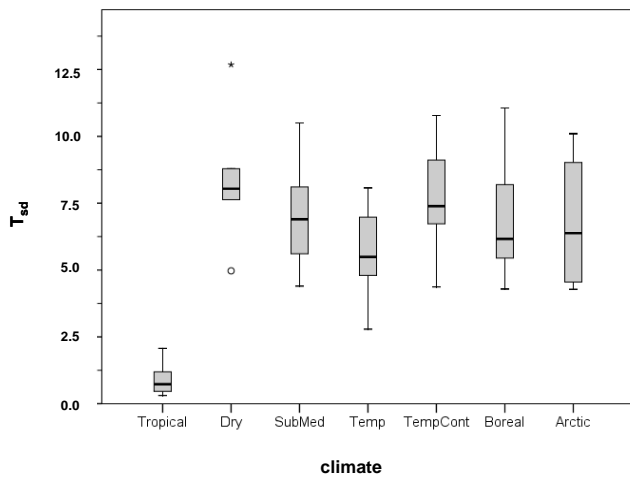


Fig. 2. Annual variation of soil temperature (T_{sd}) in different climatic regions. Boxplots for 172 Fluxnet sites as grouped to the different bioclimatic regions. $n=7, 6, 47, 49, 35, 24$ and 4 for tropical, dry, subtropical/Mediterranean, temperate, temperate continental, boreal and arctic climates, respectively.

remains well within the range where Q_{10} exerts a minor influence on the relationship between SR_{MAT} and SR_{annual} (Fig. 1).

Q_{10} values measured in situ have been reported to be normally in the range of 2–4 (Davidson et al., 2006a; Kirschbaum, 2006). Similarly, for the non-water limited temperate and boreal sites reported in this study Q_{10} was between 1.9 and 5.7, 90% of the values ranging between 2 and 5 (Table 1). To visualize the range of T_{sd} , Q_{10} and mean SR_{annual}/SR_{MAT} for the non-water-limited sites of our study in relation to the theoretical relationships, the respective data were included in Fig. 1. For clarity of the graph, Q_{10} was grouped to classes of 1–2, 2–3, 3–4 and >4 . When the observed values match the theoretical relationship very closely, reported Q_{10} values of 1–2 should thus fall in between the lines depicted for $Q_{10}=1$ and 2, and so on. The correspondence between data points and theoretical lines is generally poor. However, Fig. 1 clearly shows that T_{sd} falls in a range where Q_{10} is theoretically expected to have a minor effect on mean SR_{annual}/SR_{MAT} . Therefore, we hypothesize that SR_{MAT} and SR_{annual} are generally well coupled across non water-limited sites.

Using a Monte Carlo analysis we tested the hypothesized relationship between SR_{MAT} and SR_{annual} for 1000 random combinations of SR_{MAT} , T_{sd} and Q_{10} , constrained to a range of values commonly occurring across the globe (cf. methods). Our results confirm that such a relationship is theoretically likely to exist and indicate that only very few (i.e. ca. 10 out of 1000) random combinations of exceptionally high T_{sd} and Q_{10} will result in marked deviations from an overall relationship (Fig. 3). This does not reflect a bias in the Monte Carlo analysis, but is fully consistent with what is to be

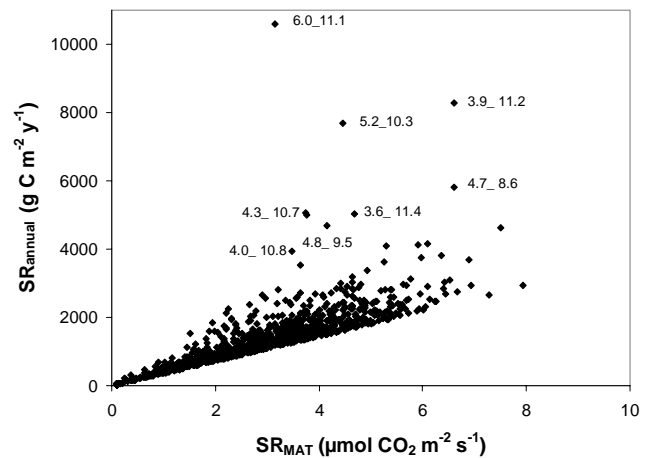


Fig. 3. Hypothetical relationship between soil respiration at mean annual temperature (SR_{MAT}) and total soil annual respiration (SR_{annual}) for 1000 random combinations of SR_{MAT} , T_{sd} and Q_{10} , as obtained by a Monte Carlo simulation. Regression: $SR_{annual}=455.8 SR_{MAT}^{1.0054}$, $R^2=0.94$, $p<0.001$. Numbers in graph indicate Q_{10} and T_{sd} for exceptionally high values of SR_{annual} .

theoretically expected (Fig. 1), because of the non-linearity of the respiration response to temperature. However, would the suggested relationship between SR_{MAT} and SR_{annual} also occur in and across real ecosystems? If so, very few measurements of SR around the mean annual temperature would be sufficient to estimate SR_{annual} .

3.2 Inter-site relationships

We tested the hypothesis first on a range of non water-limited ecosystems, including 35 sites of temperate and boreal forests and grasslands, and a tropical plantation (Table 1). Across sites we observed a highly constrained, slightly non-linear relationship between SR_{MAT} and SR_{annual} (Fig. 4a). Both theoretical considerations and field observations thus confirm the hypothesis that SR_{MAT} and SR_{annual} are tightly coupled across non water-limited sites. This striking convergence is in principle related to the inherent relationship between these parameters at likely combinations of T_{sd} and Q_{10} (Fig. 1).

To assess the robustness of our analysis we re-calculated the regression for SR_{MAT} versus SR_{annual} for the 36 non-water limited sites leaving out one site at a time (cross-validation approach). The probability density function for the 36 sites is not significantly different from a normal distribution (using a One-Sample Kolmogorov-Smirnov Test). Then we calculated the related bias for these new estimations. The mean of all the sites is 1.01 ± 0.159 (s.d.; minimum = 0.69; maximum = 1.4). The site that is underestimated is ITex (1998); and the site that is overestimated is Cow Park (UK). The results are not significantly different from the ones that we showed in the initial analysis giving

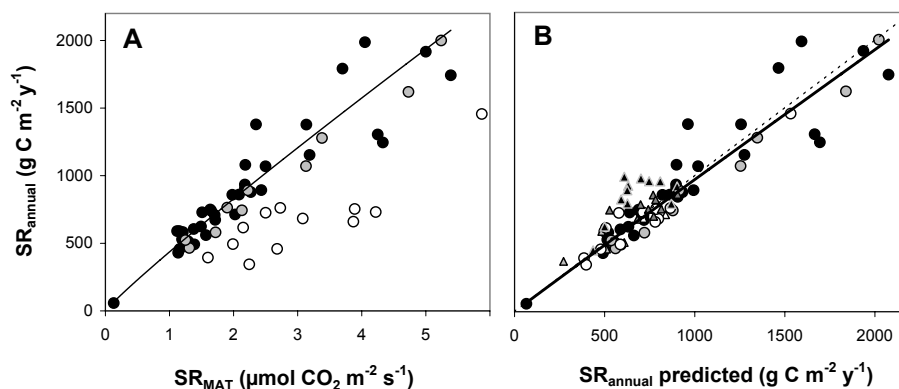


Fig. 4. (A) Relationship between soil respiration at mean annual temperature (SR_{MAT} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and total annual soil respiration (SR_{annual} , $\text{g C m}^{-2} \text{ y}^{-1}$) for 57 forests, plantations, savannas, grasslands and shrublands across boreal, temperate, tropical, mediterranean, dry sub-humid and semi-arid biomes. The regression is based on all 36 sites where precipitation/potential evapotranspiration (P/PET) exceeds 1 and no distinct dry season occurs (\bullet) ($SR_{\text{annual}} = 436.2 SR_{MAT}^{0.926}$, $R^2=0.94$, $p<0.001$). Shaded and open circles indicate seasonally dry sites where SR_{MAT} was based on annual (\bullet) and wet (\circ) season data, respectively. (B) Predicted versus observed annual soil respiration for all 80 site-years ($SR_{\text{annual observed}} = 1.06 SR_{\text{annual predicted}}^{0.988}$, $R^2=0.94$, $p<0.001$). For seasonally dry sites SR_{MAT} was corrected by an aridity factor (Fig. 5a) whenever only wet season SR_{MAT} was available. Dotted line represents the 1:1 line. Symbols as in Fig. 4a. Triangles represent the interannual data for four temperate forest sites, as shown in Fig. 6 (\blacktriangle : Harvard 1997–2008, \blacktriangle : Howland 2000–2008, \blacktriangle : Hesse 1996–1998, white \triangle : Soroe 1996–1998).

that the mean of the prediction is 1.01 at each particular site when that site is excluded. Therefore this new approach is consistent with our previous results and does not change our conclusions. The 95% confidence interval of the predictions made with the reported regressions is between 70% and 132% of the measured annual total.

We extended our analysis to seasonally dry ecosystems, including 6 seasonally dry tropical rainforests and plantations, and 15 mediterranean, dry sub-humid and semi-arid forests, savannas, grasslands and shrublands (Table 1). Irrespective of site aridity the relationship of SR_{MAT} and SR_{annual} persisted when MAT occurred during both dry and wet season, which was typically the case for all tropical sites, but also some semi-arid ecosystems (Fig. 4a). Whenever MAT occurred only during the wet season (i.e. when soil temperature exceeded MAT throughout the dry season), observed SR_{annual} was lower than would be estimated from SR_{MAT} . SR_{annual} is overestimated from SR_{MAT} measured only during the wet season, as its direct inference from SR_{MAT} does not account for the fact that during the dry season SR may be substantially reduced due to water limitations. This reduction can be corrected for (Fig. 4b), since it is strongly related to site aridity, as expressed by the ratio P/PET (Fig. 5a) or the number of months when $P/PET < 1$ (Fig. 5b). However, it should be noted that a general aridity index does not account for the interannual variability of precipitation, which may decisively alter seasonal patterns and thus the annual total of SR (Ma et al., 2007). Clearly, more studies are needed that corroborate the relationships of site aridity, SR_{MAT} and SR_{annual} for seasonally dry ecosystems.

We tested the model output against the observed values (Fig. 4b) using a paired t-test. First, we only used the 36 non water-limited sites with the predicted values from the regression without each one of the sites. There were no significant differences between observed values and predicted ($t = -0.032$, $P = 0.974$). Then we calculated the changes in the P/PET correction factor, excluding case by case and recalculating the equation. Finally, the predicted annual total SR was recalculated accounting for both changes in the P/PET correction factor and the overall relationship of SR_{MAT} and SR_{annual} occurring when each of the sites is left out at a time. Again, a paired t-test did not yield any significant differences between measured and predicted values.

We estimated the prediction uncertainty for the overall dataset by calculating the root mean squared error (RMSE). For the whole dataset RMSE was $625 \text{ g C m}^{-2} \text{ y}^{-1}$ for non water-limited sites, $404 \text{ g C m}^{-2} \text{ y}^{-1}$ for sites for which an P/PET correction factor was applied, and $618 \text{ g C m}^{-2} \text{ y}^{-1}$ for all sites. Stratified by four flux levels RMSE was $203 \text{ g C m}^{-2} \text{ y}^{-1}$ ($SR_{\text{annual}} = 0\text{--}500 \text{ g C m}^{-2} \text{ y}^{-1}$), $191 \text{ g C m}^{-2} \text{ y}^{-1}$ ($SR_{\text{annual}} = 500\text{--}1000 \text{ g C m}^{-2} \text{ y}^{-1}$), $300 \text{ g C m}^{-2} \text{ y}^{-1}$ ($SR_{\text{annual}} = 1000\text{--}1500 \text{ g C m}^{-2} \text{ y}^{-1}$) and $262 \text{ g C m}^{-2} \text{ y}^{-1}$ ($SR_{\text{annual}} = 1500\text{--}2000 \text{ g C m}^{-2} \text{ y}^{-1}$), corresponding to a relative error of 51, 27, 24 and 14%, respectively. In comparison, within-site uncertainty estimates of annual SR have been reported to be in the range of 9–25%, in some instances even up to 40–90% of SR_{annual} (Bahn et al., 2008).

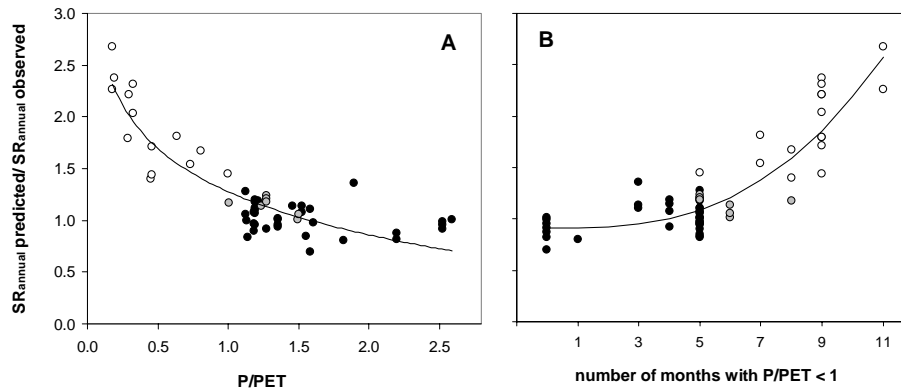


Fig. 5. Ratio of predicted to observed annual soil respiration (SR_{annual}) in relation to site aridity, as expressed by (A) the ratio of precipitation to potential evapotranspiration (P/PET) and (B) the number of dry months ($P/PET < 1$). Symbols as in Fig. 4. Regression equations and statistics for (A): $SR_{\text{annual predicted/observed}} = -0.601 \ln(P/PET) + 1.278$, $R^2 = 0.82$, $p < 0.001$; for (B): $SR_{\text{annual predicted/observed}} = 1.92 \cdot 10^{-3} x^{2.823} + 0.908$, where x is the number of months with $P/PET < 1$ ($R^2 = 0.78$, $p < 0.001$).

3.3 Interannual variation

It has been demonstrated that cross-site relationships may not reflect well within-site variability and may thus not be well suitable for deriving estimates for individual sites (for below-ground C allocation see e.g. Gower et al., 1996; Litton et al., 2007). As shown above, the inter-site relationship is robust and the 95% confidence interval of the predictions made with the reported regressions is between 70% and 132% of the correct annual total, as based on a cross-validation approach leaving out one site at a time.

Using the cross-site relationship, SR_{MAT} obtained across years within a single site predicts SR_{annual} similarly as does SR_{MAT} from across sites (Fig. 4b). RMSE for the two sites with larger number of site years, Howland Forest (9 years) and Harvard Forest (12 years), amounts to 204 and 219 $\text{g C m}^{-2} \text{y}^{-1}$, respectively, corresponding to a relative error of 26% in both cases. Thus, measurement of SR_{MAT} in any of these years would have provided an estimate of SR_{annual} within the prediction uncertainty of the cross-site relationship (cf. above). This likely holds also for exceptionally dry years or seasons, as occurred at Harvard forest in 1997 and 1999 (Fig. 6). Nevertheless, it should again be stressed that at arid sites, a fixed correction factor relating to average site aridity, may fail to account for effects caused by a distinct interannual (i.e. year-to-year) variation in precipitation (cf. above).

Figure 6 shows that within-site relationships between SR_{MAT} and SR_{annual} , as based on the available site-years for four temperate forest sites, may or may not follow the trend observed across sites, the slope differing most distinctly for Howland forest, where also only a minor amount of the inter-annual variation was explained by the regression. This may also have to do with the fact that at this site the interannual variation of SR_{annual} was comparatively small (Fig. 6). Thus,

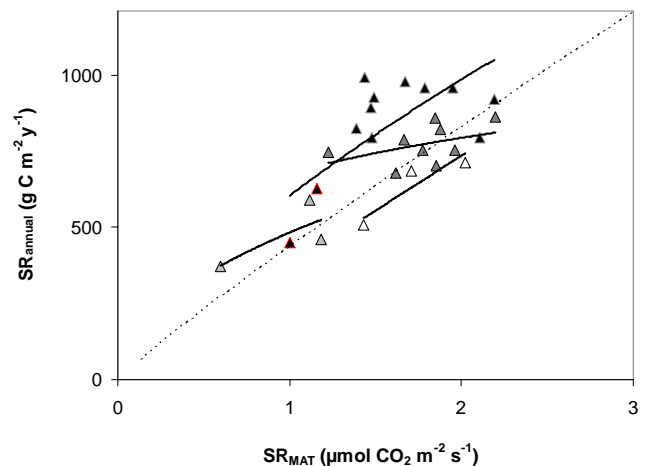


Fig. 6. Interannual variation of soil respiration at mean annual temperature (SR_{MAT} , $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and total annual soil respiration (SR_{annual} , $\text{g C m}^{-2} \text{y}^{-1}$) for four temperate forest sites (\blacktriangle : Harvard 1997–2008, \blacktriangle : Howland 2000–2008, \triangle : Hesse 1996–1998, \triangle : Soroe 1996–1998). Data for Harvard forest include two exceptionally dry summers (marked by red outlines). The dotted line indicates the cross-site relationship between SR_{MAT} and SR_{annual} data, as shown in Fig. 4a.

the cross-site relationship between SR_{MAT} and SR_{annual} may not be well suited for estimating the interannual variation of SR_{annual} , though it may provide an indication of trends if this variation is large. However, such trends are likely obscured by the comparatively large overall prediction uncertainties discussed above.

4 General implications and conclusions

Our findings have implications for assessing the spatial variability of SR_{annual} . Methodological designs typically face a trade-off between the temporal resolution required to obtain a defensible annual estimate and spatial coverage (Savage and Davidson, 2003), which has up to now resulted in estimates of SR_{annual} for a limited number of ecosystems. However, it has been shown that the spatial variability of SR may be at least of similar order of magnitude as the temporal one (Curiel Yuste et al., 2004; Kang et al., 2003; Rayment and Jarvis, 2000), which restricts our potential of estimating SR and its variation on larger spatial scales. The tight relationship between SR_{MAT} and SR_{annual} indicates that it is sufficient to assess SR_{MAT} for obtaining a highly constrained estimate of its annual total (Fig. 4b), as based on a small number of measurements. Such measurements should take into account that SR_{MAT} may vary during the year, most obviously for seasonally dry ecosystems (cf. above) but also for non water-limited ecosystems, where SR may be higher in springtime, when rhizosphere activity is high, and comparatively lower in fall (Curiel Yuste et al., 2004; Davidson et al., 2006a). Once available, SR_{MAT} not only characterizes the site-specific conditions (including climate and vegetation related effects on productivity and soil organic matter quality) for autotrophic and heterotrophic respiratory CO_2 losses, but also permits a direct estimate of SR_{annual} .

However, it should be noted that estimates for SR_{annual} obtained from SR_{MAT} will inevitably be less accurate than values obtained from episodic or even continuous datasets. The likelihood of detecting significant differences of SR_{annual} across sites and, within sites across years, will increase with an increasing variability of SR_{annual} . Thus, for assessing SR on larger scales the $SR_{\text{MAT}}-SR_{\text{annual}}$ relationship could be applied pursuing a stratified approach, which helps with identifying regional components of larger versus smaller variability in SR. If needed on a more refined scale, sites characterized by smaller variability can then be analysed in more detail, implementing more elaborate and time-consuming studies.

We conclude that soil respiration at mean annual temperature is a suitable predictor of its annual total across vegetation types and biomes. This should substantially increase our capacity for assessing the spatial distribution of annual soil CO_2 emissions across ecosystems, landscapes and regions, and thereby contribute to improving the spatial resolution of a major component of the global carbon cycle.

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