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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. There still exist considerable uncertainties as to its actual magnitude, as well as its spatial and interannual variability. Based on a reanalysis and synthesis 5 of 72 site-years for 58 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 convergence is to be 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 precipita-10 tion (P) is lower than potential evapotranspiration (PET), annual SR can be predicted from wet season SRMAT corrected for a factor related to P/PET. Our finding indicates that it is sufficient to measure SR_{MAT} for obtaining a highly constrained estimate of its annual total. This should substantially increase our capacity for assessing the spatial distribution and interannual variation of soil CO₂ emissions across ecosystems, land-15 scapes and regions, and thereby contribute to improving the spatio-temporal 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). Global estimates suggest that soils emit 68–80 Pg C per year, which exceeds emission rates from fossil fuel combustion by an order of magnitude (Denman et al., 2007; Raich and Potter, 1995; Raich et al., 2002). While indicating that soils are the predominant source of CO₂ from terrestrial ecosystems, such estimates are still highly uncertain. They are based on a very restricted dataset, which heavily underrepresents not only many biomes, but also the considerable spatial and temporal variability of SR within any given biome.

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Recently, progress has been made in illuminating factors determining the seasonal and interannual variability of SR within ecosystems (Davidson et al., 2006a). 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 5 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). 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 (Raich and Nadelhoffer, 1989; Davidson et al., 2002) and productivity in-

- dices, 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 use a theoretical framework and existing databases of SR for 58 forests, plantations, savannas, shrublands and grasslands from boreal to tropical climates, including 72 site-years, to demonstrate that SR measured at mean annual temperature (SR_{MAT}) may be a useful and meaningful predictor of SR. We further demonstrate that for seasonally dry.
- and meaningful predictor of SR_{annual}. We further demonstrate 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 potential evapotranspiration to precipitation.

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2 Methods

2.1 Database

The soil respiration database consisted of 35 sites and 49 site-years for temperate and boreal forests and grasslands, 8 tropical forests and plantations, and 15 mediterranean,

- ⁵ dry sub-humid and semi-arid forests, savannas, grasslands and shrublands, as summarized in Table 1. The database includes also 11 previously unpublished datasets, which were obtained using a range of closed and open dynamic soil respiration systems on previously installed shallow collars. Details on the systems used at the respective sites are provided in Table 2. In parallel to soil respiration measurements, soil tem-
- ¹⁰ perature (using soil temperature probes) and soil moisture (using TDR probes) were recorded. SR_{MAT} all sites and years were calculated using the reported soil temperature - respiration response functions. Calculated SR_{MAT} was cross-checked against SR values actually measured at MAT. T_{sd} was calculated from the original data records as *sd* of daily means of soil temperature for the reported years.
- ¹⁵ A global overview of T_{sd} was obtained from the Fluxnet data base (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. T_{sd} was calculated as *sd* of daily means of soil temperature. For sites reporting multiple years of soil temperature an average T_{sd} of all reported years was used.

Potential evapotranspiration (PET) was calculated according to the Modified-Hargreaves method (Droogers and Allen, 2002). This method takes in account as predictors potential radiation (top of atmosphere), average air temperature (2 m), the diurnal temperature range as well as precipitation. Global monthly grids at 0.5° reso-

²⁵ lution were calculated and extracted for each site from the grid cell closest to the site. Air temperature grids are derived from CRU climate data (New et al., 2002), homogenized and extended to 2007 (Österle et al., 2003). Precipitation data is from the GPCC project (cf. gpcc.dwd.de for documentation). For each location potential evapotranspi-

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ration 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; $MAP_{predicted} = 1.02*MAP_{measured}$, $R^2 = 0.88$).

2.2 Monte Carlo analysis

⁵ The Monte Carlo analysis for testing the hypothesized relationship between SR_{MAT} and SR_{annual} was based on 1000 random combinations of SR_{MAT} (range 0– $8.0 \,\mu$ mol m⁻² s⁻¹), T_{sd} (2–15°C) and Q_{10} (1.0–6.0).

3 Results and discussion

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Major drivers of SR include abiotic (temperature, soil moisture) and biotic (gross primary productivity) factors (Davidson et al., 2006a; Trumbore, 2006; Bahn et al., 2009). 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, SR_{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 ogeneralized 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 SR_{annual}. In this case SR at mean annual temperature (SR_{MAT}) scales directly to SR_{annual}, and their ratio expressed on the same basis (i.e. mean SR_{annual}/SR_{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 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 SR_{annual}/SR_{MAT} increases with increasing T_{sd} (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). A recently emerging global dataset of sites (Fluxnet; http://www.fluxdata.org/default.aspx;

- ⁵ Centry emerging global dataset of sites (Puxnet, http://www.luxdata.org/delault.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 remains well within the range where Q_{10} exerts a minor influence on the relationship between SR_{MAT} and SR_{annual} (Fig. 1). We therefore hypothesize that SR_{MAT} and SR_{annual} are generally tightly coupled across non water-limited sites.
- Using a Monte Carlo analysis we tested the hypothesized relationship between ¹⁵ 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. Our results confirm that such a relationship is theoretically likely to exist and indicate that only very few combinations of exceptionally high T_{sd} and Q_{10} will result in marked deviations from an overall relationship (Fig. 3). However, would this theoretical relationship also occur in ²⁰ reality? If so, very few measurements around mean annual temperature would suffice to estimate SR_{annual}.

We tested the hypothesis first on a range of non-droughted ecosystems, including 36 sites of temperate and boreal forests, grasslands and a tropical plantation (Table 1). For these sites T_{sd} and Q_{10} were in the range of 1.4 to 8.5°C and 1.9 to 6.3, respectively.

²⁵ 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).



As expected, the observed relationship between SR_{MAT} and SR_{annual} is not only also valid across different sites, but also across years differing in MAT and SR within a single ecosystem (Fig. 4a).

- We extended our analysis to seasonally dry ecosystems, including 7 seasonally dry
 tropical rainforests and plantations, and 15 mediterranean, dry sub-humid and semiarid 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,
 SR_{annual} was lower than would be estimated from SR_{MAT}. 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.

Our findings have implications for assessing the spatial and interannual 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 at 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

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activity is high, and comparatively lower in fall (Davidson et al., 2006a; Curiel Yuste et al., 2004). 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 CO₂ losses, but also permits a direct estimate of SR_{annual}.

4 Conclusions

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 and interannual variation of annual soil CO_2 emissions across ecosystems, landscapes and regions, and thereby contribute to improving the spatio-temporal resolution of a major component of the global carbon cycle.

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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., 2006, 7... Roupsard and Epron, unpublished, 8... Salimon et al., 2004, 9... Davidson et al., 2008, 10... Davidson et al., 2000, 11... Nouvellon and Epron, unpublished, 12... Nouvellon and Epron, unpublished, 13... Misson, unpublished, 14... Gimeno et al., unpublished, 15... Tang and Baldocchi, 2005, 16... Wieser et al., 2009, 17... Vargas and Allen, 2008, 18... Carbone and Trumbore, unpublished, 19... Grünzweig et al., 2009, 20... Talmon and Grünzweig, unpublished.

Site	Vegetation	Location	MAT (<i>sd</i>) (°C)	MAP (mm)	P/PET (-)	Q ₁₀ (-)	SR_{MAT} (μ mol CO ₂ m ⁻² s ⁻¹)	SR_{annual} (g C m ⁻² y ⁻¹)	Ref
Boreal and tempera	Boreal and temperate grasslands and forests								
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	Fagus sylvatica forest	41°52' N 13°38' E	2.5 (–)	1100	1.12	2.2	2.27	879	2
ITex	Picea abies, Pinus cembra forest	46°35' N 11°26' E	4.0 (6.1)	1010	1.58	3.4	2.35	1379	2
BE1Douglas	Fagus sylvatica, Pseudotsuga forest	50°18' N 6°00' E	8.1 (4.8)	1000	1.53	3.0	1.14	430	2
BE1beech	Fagus sylvatica, Pseudotsuga forest	50°18' N 6°00' E	8.1 (4.8)	1000	1.53	2.4	2.20	844	2
FR1	Fagus sylvatica forest	48°40' N 7°05' E	9.4 (4.7)	820	1.32	4.0	2.02	713	2
DK	Fagus sylvatica forest	56°00' N 12°20' E	7.4 (4.6)	600	1.18	5.0	1.12	590	2
GE1-47y	Picea abies forest	50°09' N 11°52' E	6.1 (–)	890	1.36	2.4	1.71	709	2
GE1-87y	Picea abies forest	50°09' N 11°52' E	6.1 (-)	890	1.36	3.2	1.65	740	2
GE1-111y	Picea abies forest	50°09' N 11°52' E	6.1 (–)	890	1.36	2.9	1.98	859	2
GE1-146y	Picea abies forest	50°09' N 11°52' E	6.1 (–)	890	1.36	2.4	1.49	624	2
GE-Kiel	Fagus sylvatica forest	54°06' N 10°14' E	7.6 (–)	697	1.56	3.9	1.15	590	2
SE1	Picea abies, Pinus sylvestris forest	60°05' N 17°28' E	5.7 (4.4)	530	1.14	2.8	2.18	1080	2
Bra2001A	Pinus sylvestris, Quercus robur forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	1.9	1.16	458	3
Bra2001B	Pinus sylvestris, Quercus robur forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	1.9	1.57	560	3
Bra2001C	Pinus sylvestris, Quercus robur forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	2.4	1.39	492	3
Bra2001D	Pinus sylvestris, Quercus robur forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	3.3	2.18	935	3
Bra2001E	Pinus sylvestris, Quercus robur forest	51°18' N 4°31' E	11.4 (5.1)	750	1.20	4.8	1.71	674	3
Bra2001F	Pinus sylvestris, Quercus robur forest	51°18" N 4°31' E	11.4 (5.1)	750	1.20	2.5	2.43	893	3
DK1	Fagus sylvatica forest	55°29' N 11°38' E	8.0 (4.4)	600	1.18	4.0	1.38	605	4
Dk2	Fagus sylvatica forest	56°00' N 12°20' E	8.0 (4.4)	600	1.18	4.6	1.21	583	4
Dk3	Fagus sylvatica forest	56°00' N 12°20' E	8.0 (4.4)	600	1.18	4.1	1.29	515	4
Harvard Forest	Mixed hardwood forest	42°32' N 72°11' W	9.8 (6.5)	1089	1.14	3.8	2.09	860	5
Howland	Mixed evergreen forest	45°12' N 68°44' W	6.5 (6.4)	1005	1.27	3.4	1.64	750	6

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Table 1. Continued.

			MAT (sd)	MAP	P/PET	Q ₁₀	SR _{MAT}	SR _{annual}	
Site	Vegetation	Location	(°C)	(mm)	(-)	(–)	$(\mu mol CO_2 m^{-2} s^{-1})$	$(g C m^{-2} y^{-1})$	Ref
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	7
Rio Branco	Rainforest	9°56' S 67°52' W	23.8 (0.8)	1940	1.24	5.6	4.73	1620	8
Tapajos	Rainforest	2°90' S 54°95' W	26.0 (-)	2090	1.50	-	3.38	1279	9
Paragominas	Primary forest	2°59' S 47°31' W	23.0 (0.7)	1784	1.50	1.0	5.24	2000	10
Itatinga	Eucalytus plantation	23°01' S 48°32' W	19.1 (2.0)	1360	1.01	-	3.13	1071	11
Kondi	Eucalytus plantation, 5 y	4°35' S 11°75' E	25.8 (2.0)	1400	1.27	-	1.31	465	12
Kondi	Eucalytus plantation, 13 y	4°35′ S 11°75′ E	25.8 (2.0)	1400	1.27	-	2.13	744	12
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	13
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	14
Savanna grassland open	Savanna grass	38°43' N 120°96' W	17.7 (6.9)	496	0.46	1.1	1.60	394	15
Savanna trees	Quercus douglasii	38°43' N 120°96' W	17.7 (6.9)	496	0.46	1.2	2.15	616	15
Tenerife	Pinus canariensis forest	28°35' N 27°15' W	10.4 (4.2)	460	0.45	3.89	2.50	726	16
James Reserve woody	Mixed conifer and oak	33°48' N 116°46' W	11.8 (6.7)	507	0.30	1.7	1.9	764	17
James Reserve herb.	Eriogonum wrightii	33°48' N 116°46' W	10.8 (7.9)	507	0.30	1.7	1.25	524	17
James Reserve forest	Quercus /Pinus forest	33°48' N 116°46' W	9.0 (6.6)	507	0.30	-	4.05	892	18
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	19
Semi-arid shrubland	Sarcopoterium spinosum	31°23' N 34°54' E	21.7 (7.6)	300	0.18	1.6	4.22	731	20
Semi-arid shrubland	Intershrub microsite	31°23' N 34°54' E	22.9 (8.9)	300	0.18	1.4	2.25	345	20
Dry subhumid shrubland	Sarcopoterium spinosum	31°42' N 35°03' E	19.1 (6.6)	540	0.32	1.6	3.89	754	20
Dry subhumid shrubland	Intershrub microsite	31°42' N 35°03' E	21.2 (8.2)	540	0.32	1.8	3.87	660	20

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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)	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

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Fig. 1. The ratio of mean annual soil respiration (mean SR_{annual} , $\mu mol m^{-2} s^{-1}$) to soil respiration at mean annual temperature (SR_{MAT} , $\mu mol m^{-2} s^{-1}$) 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 SR_{annual}/SR_{MAT} , T_{sd} and Q_{10} classes.











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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}, R²=0.94, ρ <0.001. Numbers in graph indicate Q_{10} and T_{sd} for exceptionally high values of SR_{annual}.



Fig. 4. (A) Relationship between soil respiration at mean annual temperature (SR_{MAT}, μ mol CO₂ m⁻² s⁻¹) and total annual soil respiration (SR_{annual}, gCm⁻² y⁻¹) for 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 (closed circles: •) (SR_{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 (•) and wet (\odot) season data, respectively. Triangles represent the interannual data for four temperate forest sites (**A** Harvard 2005–2008, **A** Howland 2000–2008, **A** Hesse 1996–1998, Δ Soroe 1996–1998). (**B**) Predicted *versus* observed annual soil respiration for all 72 site-years (SR_{annual} observed=1.06 SR_{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.

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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_{annual} predicted/observed=-0.601 Ln(P/PET)+1.278, $R^2=0.82$, p<0.001; for (B): SRannual predicted/ observed= $1.92 \ 10^{-3} x^{2.823}+0.908$, where x is the number of months with P/PET<1 ($R^2=0.78$, p<0.001).

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