Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices

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[1]   Field-chamber measurements of soil respiration from 17 different forest and shrubland sites in Europe and North America were summarized and analyzed with the goal to develop a model describing seasonal, interannual and spatial variability of soil respiration as affected by water availability, temperature, and site properties. The analysis was performed at a daily and at a monthly time step. With the daily time step, the relative soil water content in the upper soil layer expressed as a fraction of field capacity was a good predictor of soil respiration at all sites. Among the site variables tested, those related to site productivity (e.g., leaf area index) correlated significantly with soil respiration, while carbon pool variables like standing biomass or the litter and soil carbon stocks did not show a clear relationship with soil respiration. Furthermore, it was evidenced that the effect of precipitation on soil respiration stretched beyond its direct effect via soil moisture. A general statistical nonlinear regression model was developed to describe soil respiration as dependent on soil temperature, soil water content, and site-specific maximum leaf area index. The model explained nearly two thirds of the temporal and intersite variability of soil respiration with a mean absolute error of $0.82 \; \mu\text{mol m}^{-2} \text{ s}^{-1}$. The parameterized model exhibits the following principal properties: (1) At a relative amount of upper-layer soil water of 16% of field capacity, half-maximal soil respiration rates are reached. (2) The apparent temperature sensitivity of soil respiration measured as Q_{10} varies between 1 and 5 depending on soil temperature and water content. (3) Soil respiration under reference moisture and temperature conditions is linearly related to maximum site leaf area index. At a monthly timescale, we employed the approach by *Raich et al.* [2002] that used monthly precipitation and air temperature to globally predict soil respiration (T&P model). While this model was able to explain some of the month-to-month variability of soil respiration, it failed to capture the intersite variability, regardless of whether the original or a new optimized model parameterization was used. In both cases, the residuals were strongly related to maximum site leaf area

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index. Thus, for a monthly timescale, we developed a simple T&P&LAI model that includes leaf area index as an additional predictor of soil respiration. This extended but still simple model performed nearly as well as the more detailed time step model and explained 50% of the overall and 65% of the site-to-site variability. Consequently, better estimates of globally distributed soil respiration should be obtained with the new model driven by satellite estimates of leaf area index. Before application at the continental or global scale, this approach should be further tested in boreal, cold-temperate, and tropical biomes as well as for non-woody vegetation.   *INDEX TERMS:* 1615 Global Change: Biogeochemical processes (4805); 3210 Mathematical Geophysics: Modeling; *KEYWORDS:* carbon balance, drought, leaf area index

1.   Introduction

[2]   Given that terrestrial ecosystems take up about one third of the CO_2 emissions from anthropogenic fossil fuel burning and cement manufacture [*Schimel et al.*, 2001], it is critical to improve our knowledge and understanding of the carbon exchange between terrestrial ecosystems and the atmosphere. With globally 68–80 Pg C yr^{-1}, soil respiration represents the second largest carbon flux between ecosystems and the atmosphere [*Raich and Schlesinger*, 1992; *Raich and Potter*, 1995; *Raich et al.*, 2002]. This amount is more than 10 times the current rate of fossil fuel combustion and indicates that each year, around 10% of the atmosphere's CO_2 cycles through the soil. Thus, even a small change in soil respiration could significantly intensify, or mitigate, current atmospheric increases of CO_2, with potential feedbacks to climate change. Despite this global significance as well as considerable scientific commitment to its study over the last decades, there is still limited understanding of the factors controlling temporal and across-ecosystem variability of soil respiration.

[3]   Important factors influencing soil respiration include (1) soil temperature [*Singh and Gupta*, 1977; *Lloyd and Taylor*, 1994; *Kirschbaum*, 1995; *Kätterer et al.*, 1998; *Reichstein et al.*, 2000], (2) soil water status [*Carlyle and Bathan*, 1988; *Howard and Howard*, 1993], (3) net primary or net ecosystem productivity [*Norman et al.*, 1992; *Raich and Potter*, 1995; *Janssens et al.*, 2001], (4) substrate quality [*Raich and Schlesinger*, 1992], (5) land-use and disturbance regimes [*Ewel et al.*, 1987], and (6) population and community dynamics of the above- and belowground flora and fauna [*Raich and Schlesinger*, 1992]. Since a bottom-up modeling of all these complex interactions is unfeasible particularly at larger spatial scales, models have to implement simpler relations empirically derived from field studies. Thus, soil respiration is often modeled as a simple Q_{10} or Arhennius-type function of temperature, and sometimes multiplicatively modified by a scalar dependent on water availability. One example is the approach by Raich and coworkers, who predict globally distributed soil respiration from monthly air temperature and precipitation [*Raich and Potter*, 1995; *Raich et al.*, 2002].

[4]   Regardless of the simplicity of models, there are two issues that still lead to uncertainties in current and future estimates of soil respiration. (1) Most analyses, reviews, and models have built on data sets that under-represent water-limited sites [*Lloyd and Taylor*, 1994; *Raich and Potter*, 1995; *Janssens et al.*, 2003], leading to a potential under-estimation of drought effects on respiration. (2) The common assumption of an invariable temperature sensitivity of decomposition/respiration is questionable since *Liski et al.* [1999] indicated dependencies on soil organic matter age, and *Reichstein et al.* [2002a] found declining temperature sensitivity of respiration with increasing soil water deficit. This issue of temperature sensitivity is particularly important, since recent simulation results, that are showing a switch of the terrestrial biosphere from a carbon sink to a source within this century [*Cox et al.*, 2000], are much contingent on the fixed parameterization of $Q_{10} = 2.0$ (P. M. Cox, personal communication, 2001).

[5]   Thus the following study builds on 17 recently emerging soil respiration data sets at sites that experience seasonal drought (mostly from FLUXNET activities [*Baldocchi et al.*, 2001]). The strength of the data sets examined here is that not only soil respiration but also a number of ecosystem properties and processes were measured simultaneously, and in a relatively standardized manner. Factors contributing to temporal and site-to-site variability are analyzed with the final goal to develop models able to explain temporal and site-to-site variability at daily and monthly time steps with predictors that are available at continental to global scale.

2.   Materials and Methods

2.1.   Site Description

[6]   The study includes a range of sites from Europe and North America all subject to drought for part of the year, including sand and clay soils with low and high rock fraction, deciduous and evergreen forests and open woodland and shrubland with leaf area index ranging from 0.8 to 4.8 and annual precipitation from 270 to 1608 mm (Table 1). Two sites (C, P) are dominated by *Quercus ilex*, two (M, T) by *Pinus halepensis*, three sites (L, O, Y) by *Pinus ponderosa*, one (B) by *Pinus pinaster*, and six sites (0–4, N) by deciduous oaks (*Quercus cerris, Q. robur*). The sites Arca di Noè (A) and Sky Oaks Young (S) are multispecies shrubland sites, while Èvora (E) is a savannah-type ecosystem (dehesa) with a dense seasonal grass layer and evergreen broad-leaf oak trees (*Quercus ilex* L./ *Qu. suber*). The sites at Rocca (0–4) represent a chronosequence of a rotation forest (coppice). Thus all major woody

Table 1. Study Sites (Sorted by Longitude) and Their Characteristics[a]

Site Name/Country[b]	Site Label	Latitude°	Longitude°	LAI m² m⁻² ($m^2 m^{-2}$)	Leaf Litterfall gC m⁻² yr⁻¹	Leaf Production gC m⁻² yr⁻¹	Total C_{soil} kgC m⁻²	C_{litter} kgC m⁻²	C/N_{litter} gC g⁻¹N	C/N_{soil} gC g⁻¹N	Aboveground Biomass kgC m⁻²	Leaf Biomass gC m⁻²	Annual Avg. Precipitation mm	Annual Air Temperature °C	R_{ref} (in Equation (2)) μmol m⁻² s⁻¹	Vegetation Type[c]	Years of Observation
Metolius old/USA	O	44.50	−121.62	2.1	132	76	5.9	1.23	89.0	17.8	10.8	286	524	8.1	4.73	ENF	1999–2000
Metolius young/USA	Y	44.44	−121.57	1.0	50	23	4.3	0.71	96.0	8.6	0.9	117	552	7.5	3.78	ENF	1999–2000
Blodgett forest/USA	L	38.90	−120.63	2.7	96	177	27.3	NA	NA	9.8	0.9	355	1608	11.3	6.01	ENF	1998–1999
Sky oaks/USA	S	33.37	−116.62	1.1	33.4	72	0.87	0.05	NA	NA	0.6	108	491	12.2	0.78	SHB	1999–2001
Évora/Portugal	E	38.54	−8.00	1.6	48	36	2.5	NA	53.8	11.2	NA	70	658	16.0	4.34	SAV	2000
Maials/Spain	M	41.37	0.37	0.8	49	49	11.6	2.06	103.0	16.2	NA	98	388	15.2	1.45	ENF	1995–1996
Le Bray/France	B	44.72	0.77	4.8	272	255	15.0	1.45	61.0	26.6	6.5	480	955	12.9	6.91	ENF	2000–2001
Puéchabon/France	P	43.74	3.60	2.9	114	160	6.1	0.34	54.0	14.8	5.6	321	883	13.4	3.87	EBF	1999
Arca di Noè/Italy	A	40.61	8.15	1.6	63	64	10.0	NA	58.1	NA	0.5	143	643	16.8	2.29	SHB	1998–1999
Nonantola/Italy	N	44.69	11.09	2.0	81	81	4.8	0.08	NA	NA	6.6	81	1000	14.5	3.62	DBF	2001
Rocca 0 years/Italy	0	42.39	11.92	3.3	147	147	9.5	NA	NA	14.0	1.5	147	936	14.4	5.95	DBF	1999
Rocca 2 years/Italy	1	42.39	11.92	3.4	149	149	9.5	2.24	NA	NA	1.6	149	936	14.4	5.53	DBF	1999–2000
Rocca 8 years/Italy	2	42.39	11.92	4.3	191	191	8.9	2.37	NA	35.8	4.4	191	936	14.4	8.05	DBF	1999–2000
Rocca 15 years/Italy	3	42.41	11.93	4.5	198	198	7.0	1.29	NA	NA	6.8	198	936	14.4	4.90	DBF	1999–2000
Rocca 20 years/Italy	4	42.41	11.93	3.8	168	168	8.3	1.54	NA	9.2	5.6	168	936	14.4	7.50	DBF	1999–2000
Castelporziano/Italy	C	41.71	12.38	3.5	145	145	NA	NA	NA	12.3	NA	290	740	15.5	5.13	EBF	2000–2001
Yatir/Israel	T	31.35	35.05	2.0	50	53	3.7	0.10	64.4	11.0	1.4	150	270	18.0	2.97	ENF	2000–2002

[a]See section 2 for details.

[b]References to the sites according to label: B: [Loustau et al., 1999]; M: [Casals et al., 2000]; E: [Pereira et al., 2001]; N: unpublished; P: [Joffre et al., 1996]; O, Y: [Law et al., 2001a, 2001b]; T: [Grunzweig et al., 2003]; 0–4: [Rey et al., 2003]; A: [Benincasa et al., 1999]; C: [Manes et al., 1997]; S: [Qian et al., 2001]; L: [Xu and Qi, 2001a, 2001b].

[c]Abbreviations: ENF, Evergreen needleleaf forest; EBF, Evergreen broad-leaf forest; SAV, savannah; DBF, deciduous broad-leaf forest; SHB, shrub-land.

biome types in temperate and Mediterranean climate are represented in this study. See Table 1 and references therein for more site-specific information.

2.2. Data Collection and Treatment

[7] Soil respiration was measured using closed-dynamic chamber techniques with an infrared gas analyzer (exception: Maials: NaOH trap technique). Spatial replicates were averaged and then aggregated to one value per day resulting in a total of 547 days of soil respiration estimates. Intercalibration of the different chamber techniques was not possible; thus the flux data from each site were used without corrections. However, since closed chambers were used at all sites, the among-site error when comparing fluxes should be small. This has also been proven recently by *Pumpanen et al.* [2003], who compared the performance of several respiration chambers, among them a number of chamber types that have been used for the respiration measurements in this study, via an absolute calibration system. The NaOH-technique has been shown to give biased estimates of soil respiration, though mainly at high respiration rates that do not occur at the Maials site [*Pongracic et al.*, 1997]. Hence we analyzed the data with and without the Maials site and present results of both analyses in the tables, while in the figures we show the results including all sites (nevertheless, the site can be identified by the label).

[8] Soil temperature was measured inside or near the respective soil chamber at 10 cm depth (5 cm at Yatir site). Soil water content was observed as volumetric water content (%) with time domain reflectometry (TDR) sensors over 0 to 20 cm or 0 to 30 cm depth. At the Maials (M), Nonantola (N), and Yatir (T) sites, soil water content was determined gravimetrically and subsequently transformed into volumetric moisture by multiplication with soil bulk density. Volumetric water content is not a good measure of water availability when soils of different texture and stone content are compared. Theoretically, soil water matrix potential provides such a good measure of water availability and allow comparison between different soils. However, the calculation of soil water potential from soil water content is prone to large errors, particularly in dry soils [*Rawls and Brakensiek*, 1989]. Furthermore, theoretical reasons against using soil water potential as a predictor for soil respiration have been raised [*Orchard and Cook*, 1983], although more recent studies do indicate its usefulness [e.g., *Irvine and Law*, 2002]. Thus, relative soil water content (RSWC) defined as the amount of water available relative to the amount of water at field capacity (SWC_{FC}) was employed here as a general measure of soil water availability:

$$RSWC = \frac{SWC}{SWC_{FC}}, \qquad (1)$$

where SWC is the actual soil water content (m^3 m^{-3}), while SWC_{FC} is the soil water content at field capacity (approximated as the soil water content after 3 days of drainage after maximum soil water content was reached). When SWC_{FC} could not be estimated in this manner, it was estimated with a soil water balance model (PROXEL-SOIL

[*Reichstein et al.*, 2002a]), calculating the drainage for 3 days after strong rain according to texture dependent soil parameters [*Rawls and Brakensiek*, 1989].

2.3. Site Variables

[9] The following site variables were used in the analysis and determined as follows: (1) Leaf area index (m^2 m^{-2}) was either measured by harvest (sites A, O, Y, grass layer E), by determining the leaf litter area (site M), or via extinction of diffuse radiation using a leaf area meter LICOR-2000 (other sites). Where significantly present, the understory was included into the estimate of leaf area index. (2) Leaf biomass (gC m^{-2}) was either determined by harvest (sites A, Y, O), leaf litter fall (M, P), or estimated from leaf area index through multiplication with leaf carbon mass per area [*Damesin et al.*, 1997]. Then, species specific carbon mass per area values were taken from *Bussotti et al.* [2000] where not available from the site. (3) Leaf productivity (gC m^{-2} yr^{-1}) was estimated as the product of leaf biomass and the inverse leaf life span (i.e., leaf turnover). Leaf life span was extracted species-specifically from the literature [*Orshan*, 1989] if not directly available from the sites. (4) Aboveground biomass was either determined by harvest (sites A, O, Y) or estimated from tree diameter and height via site-specific tables. (5) Soil carbon storage was determined separately for organic layer(s) and the mineral soil. At the multispecies sites Arca di Noè, Sky Oaks, and Metolius (A, S, Y, O), the vegetation parameters were determined for each species and then summed up to give a representative value for the whole community. At the Èvora site (E), which is a Mediterranean savannah-type ecosystem (dehesa), the grass layer was included in all the calculations.

2.4. Models: Daily Time Step

[10] The modeling of soil respiration at the daily time step follows the logic that the main abiotic drivers that determine soil respiration are soil temperature (T_{soil}) and soil water availability, that can be expressed as soil water content relative to the soil water content at field capacity (RSWC). Accordingly, the soil respiration (R, μmol m^{-2} s^{-1}) data were analyzed using a nonlinear regression model as follows:

$$R = R_{ref} \cdot f(T_{soil}, RSWC) \cdot g(RSWC), \qquad (2)$$

$$f(T_{soil}, RSWC) = e^{E_0(RSWC) \cdot \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{soil} - T_0} \right)}, \qquad (3)$$

$$g(RSWC) = \frac{RSWC}{RSWC_{1/2} + RSWC}, \qquad (4)$$

$$E_0(RSWC) = a_{REW} + b_{REW} \cdot RSWC. \qquad (5)$$

[11] In these equations, R_{ref} (μmol m^{-2} s^{-1}) is the soil respiration under standard conditions (at $T_{ref} = 18°C$; non-limiting water), E_0 (K^{-1}) is the activation-energy-type

parameter of *Lloyd and Taylor* [1994], T_{ref} (°C) is the reference temperature, T_0 (°C) is the lower temperature limit for the soil respiration R, and $RSWC_{1/2}$ (fraction) is the soil water content where half-maximal respiration (at a given temperature) occurs. In equation (5), we propose that the temperature sensitivity of soil respiration is dependent on the soil water status of the soil, where as a first approximation E_0 is linearly dependent on RSWC. *Reichstein et al.* [2002b] corroborated the same hypothesis for ecosystem respiration. T_0 was fixed at −46°C as in the original model of [*Lloyd and Taylor*, 1994], and T_{ref} was set to 18°C, which approximates the mean soil temperature at the study sites.

[12] First, the regression model was applied to each site separately, so that site-specific soil respiration rates corrected for soil temperature and soil moisture were estimated (R_{ref}). These standardized respiration rates were correlated with the other site variables in Table 1 (see below). On the basis of this analysis, in a second step a general regression model (including all sites simultaneously) was applied by adding an empirical explicit dependency of the reference respiration rate (R_{ref} in equation (2)) on maximum site leaf area index (LAI_{max}) to the regression model,

$$R_{ref}(LAI_{max}) = a_{LAI} + b_{LAI} \cdot LAI_{max}, \qquad (6)$$

similar to what has previously been applied for North American grassland sites [*Norman et al.*, 1992].

2.5. Models: Monthly Time Step

[13] At a monthly time step, we tested the model proposed by [*Raich et al.*, 2002], that predicts soil respiration from monthly average air temperature (T_a, °C) and precipitation sum (P, cm) as follows:

$$R_{month} = R_0 \cdot e^{Q \cdot T_a} \cdot \frac{P}{K + P}. \qquad (7)$$

[14] In this equation, R_{month} refers to the mean monthly soil respiration (gC m^{-2} d^{-1}), R_0 (gC m^{-2} d^{-1}) is the soil respiration at 0°C without moisture limitation, Q (°C^{-1}) determines the exponential relationship between soil respiration and temperature, and K (cm) is the half-saturation constant of the hyperbolic relationship of soil respiration with monthly precipitation. Initially, the original parameters as proposed by *Raich et al.* [2002] were employed: R_0 = 1.25 gC m^{-2} d^{-1}, Q = 0.05452°C^{-1}; K = 4.259 cm. Additionally, the model was reparameterized by calculating a nonlinear least squares fit of the parameters (R_0, Q, K) to our data set. The model is referred to here as T&P model (temperature and precipitation model), original or reparameterized.

[15] The monthly temperature and precipitation data for each site were obtained from meteorological observations directly at each site. Monthly mean soil respiration estimates were constructed in the same way as by *Raich et al.* [2002]; that is, all available respiration observations were averaged per month and site.

2.6. Statistical Estimation Technique

[16] The parameter estimation of the nonlinear regression model parameters is based on the least-sum-of-residual-squares criterion [*Draper and Smith*, 1981]. Standard errors of nonlinear regression parameters were estimated by a bootstrapping algorithm. The original data sets consisting of soil respiration, soil temperature, and relative extractable water were randomly resampled (with replacement) 500 times, where each "resample" was made up to the same number of data points as the original data set. The nonlinear regression (nonlinregress in PV-WAVE 6.21 [*Visual Numerics Inc.*, 1993]) was run for each "resample" resulting in 500 parameter estimates per original data set. The standard deviation of these 500 estimates is a good measure of the random error associated with the individual regression parameters [*Efron and Tibshirani*, 1993].

[17] Since five sites in Europe (labels 0−4 in Table 1) and two sites from North America (Y, O in Table 1) were geographically adjacent to each other, they cannot be considered statistically independent. In order to test if the results are biased toward those sites, all the regressions were also performed with only one of the adjacent sites included. In these tests the regression parameters differed only slightly from regression parameters including all sites, and were always within 1 standard error of the regression parameters including all sites.

[18] The three statistics RSME (root mean squared error), r^2 (coefficient of determination), and MEF (modeling efficiency) are used for model evaluation as defined by *Janssen and Heuberger* [1995].

3. Results and Discussion

3.1. Daily Time Step

[19] Respiration rates corrected for soil temperature and soil moisture effects (R_{ref}, i.e., at 18°C and without water limitation) ranged between 0.8 and 8.1 μmol m^{-2} s^{-1} (Table 1). Leaf area index, annual leaf litterfall, and annual leaf production are the site-specific variables that correlate most strongly with the standardized soil respiration rates (R_{ref}) (Table 3, Figure 1). On the contrary, both aboveground and belowground carbon stocks correlate only weakly with R_{ref}. This reflects the fact that not only the quantity of the carbon stock, but essentially the turnover, determines the amount of carbon decomposed and eventually released from the soil. Particularly clay soils can contain large amounts of quasi-inert carbon that is hardly accessible for microbial oxidation [e.g., *Scheffer and Schachtschabel*, 1992]. A large portion of soil respiration is likely to originate from recently assimilated carbon, namely through root/rhizosphere respiration and decomposition of fresh organic matter. The strong correlation between respiration and annual leaf production supports the hypothesis suggesting that site productivity is a major determinant of soil respiration [*Janssens et al.*, 2001]. Similarly, leaf area index can be viewed more as an indicator of the carbon assimilation potential and, thus, of the potential of how much carbon (easily available to microbes) can be translocated belowground, explaining the strong correlation of maximum leaf area index with R_{ref} (see also overall discussion below).
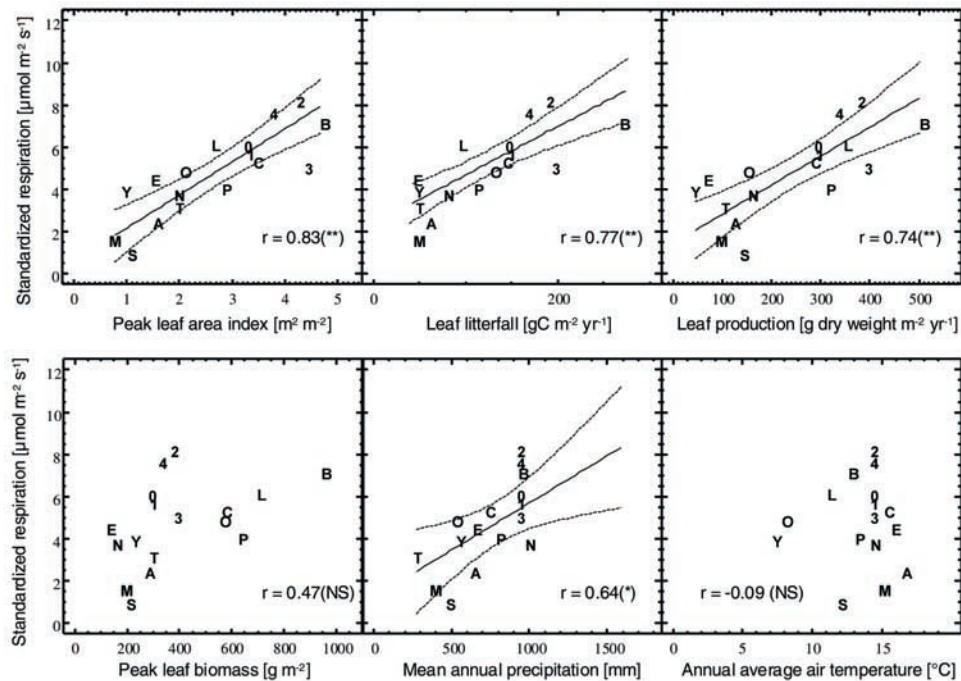
Figure 1. Relationship between site-specific parameters and soil respiration (corrected for temperature and moisture effects, i.e., parameter R_{ref} in equation (2)). Where significant, linear regression lines plus 95% confidence intervals are drawn. For site labels, see Table 1. The product-momentum correlation coefficient (r) is indicated along with level of significance (**:$p < 0.01$; *: $p < 0.05$; NS: $p > 0.05$).

[20] Furthermore, annual precipitation was significantly positively correlated with R_{ref} (Table 3; note that the latter is already corrected for soil moisture effects, i.e., with no water limitation). This means that precipitation has an indirect influence on soil respiration that superimposes on the direct limitation through soil drought. Clearly, this indirect influence is caused by the influence of precipitation on vegetation productivity, since those two variables also correlate significantly positively. Thus this result stresses the importance of precipitation for soil respiration via two pathways, the direct influence through water limitation of soil microbes and the indirect influence via site productivity. In contrast, there is no such double-effect of temperature on soil respiration for the sites studied here, since there is no correlation between mean annual air temperature and R_{ref} (Table 3). Obviously, temperature was not strongly limiting the site productivity at those sites. This latter result may be explained by the fact that the sites in this study are indeed relatively warm sites, although *Janssens et al.* [2001] also found no positive correlation between mean air temperature and annual respiration for a collection of colder sites (temperature range of mean annual temperature $4°-10°C$). In any case, these results stress the importance of water availability for site productivity and soil respiration, compared to temperature.

[21] While a correlation of standardized soil respiration with maximum site leaf area index makes sense from an ecological perspective, it may also provide a basis for improved estimates of spatially resolved global soil respiration. Leaf area index already has a strong history as an integrative var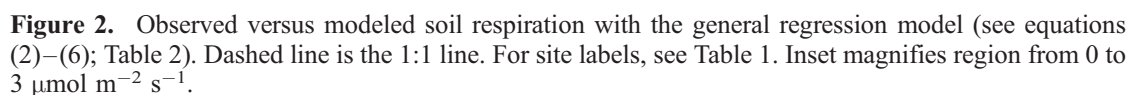iable for regional modeling of water limitation effects on vegetation productivity [*Woodward*, 1987; *Specht and Specht*, 1989] and can link remote sensing to gross and net primary productivity [*Running*, 1990]. Leaf area index being a good predictor of intersite variability of soil respiration may also provide good prospects for regional estimates of respiration from remotely sensed vegetation indices, although the relationship is not as well justified theoretically and cannot be expected to be as direct and stable as between leaf area index and gross primary productivity. Thus, such an approach will always remain more empirical and descriptive, unless more sophisticated approaches, for example, including memory and lag effects through decomposition dynamics, are employed [*Irvine and Law*, 2002]. On the other hand, it should be noted that the results obtained here were valid independent of the trajectory to reach maximum LAI from clear-cut and fire perturbation or reforestation to a given stage of maturity (even early stage in Italy Rocca sequence) and of the life history of the dominant species (obligate seeder or resprouter). Thus the inclusion of leaf area index as a predictor for soil respiration is likely to be an improvement over models that ignore vegetation structure or productivity and are purely climate driven, and should be able to capture more of the global geobiological variability of soil respiration.

[22] Thus, including a linear dependency of R_{ref} on LAI into the regression model resulted in a general model that described both intersite and temporal variability with a single set of parameters (Table 2, Figures 2 and 3). The model explains nearly two thirds of the variability with a mean absolute error below 1 μmol m^{-2} s^{-1}. From the model parameterization the following implications are apparent:

Table 2. Regression Parameters and Statistics for the General Model as Stated in Equations (3)–(6)[a]

Parameter	a_{LAI}, μmol m^{-2} s^{-1}	b_{LAI}, μmol m^{-2} s^{-1}	RSWC$_{1/2}$ (fraction)	a_{E0}, K^{-1}	b_{E0}, K^{-1}	Mean Absolute Error, μmol m^{-2} s^{-1}	RSME, μmol m^{-2} s^{-1}	r^2
Estimate (all data)	0.6 ± 0.28	1.29 ± 0.10	0.16 ± 0.02	52.4 ± 47.1	285.0 ± 67.6	0.82	1.11	0.62
NaOH-method, site Maials excluded	0.63 ± 0.23	1.27 ± 0.13	0.15 ± 0.02	49.3 ± 48.2	288.1 ± 69.3	0.84	1.13	0.60

[a]Given are parameter estimates ±1 approximate standard error.

(1) There is a strong dependency of soil respiration on soil water content. At a RSWC content of 50%, 10%, and 5%, soil respiration is reduced by 24%, 62%, and 76%, respectively. A simple relationship between soil temperature and soil respiration as often found in boreal ecosystems is not valid for water-limited sites, because the respiration can be very different at the same temperature depending on RSWC (not shown). (2) RSWC seems to be a practical general measure of soil water availability across a large range of soils with different textures and stone contents. Namely, the parameter RSWC$_{1/2}$ (0.16, water content at half-maximal respiration) did not exhibit a higher relative standard error of estimate than the other regression parameters (Table 2). (3) The apparent temperature sensitivity of soil respiration is dependent on RSWC. This is expressed as a variable [*Lloyd and Taylor*, 1994]-"activation-energy" parameter (E_0), which was significantly influenced by RSWC (b_{E0} = 285 K^{-1}, significantly different from 0). While in the original Lloyd- and -Taylor model the E_0 parameter is fixed at 308 K^{-1} (which corresponds to a Q_{10} of 2.3 at 15°C), the data of this study suggest that it varies from 50 K^{-1} in dry soil to 350 K^{-1} under well watered conditions (corresponding to Q_{10} at 15°C varying from 1.1 to 2.6). This pattern is in agreement with *Reichstein et al.* [2002a], who found the Q_{10} of ecosystem respiration varying from near 1.0 under dry to 2.5 under well-watered conditions in two Mediterranean forests. In contrast to many models that use a constant Q_{10} for the temperature dependence of respiration, the proposed model implies a nonlinear dependency of the apparent Q_{10} on both temperature and soil water content (Figure 4). Given the high sensitivity of coupled general circulation and global carbon balance models to the Q_{10} used for soil respiratory processes [*Cox et al.*, 2000], severe influences of such nonlinear responses of Q_{10} to drought and temperature on future carbon balance predictions must be expected.

[23] Despite good overall model performance (the model provided unbiased estimates of soil respiration (Figure 3) with a mean absolute error of less than 1 μmol m^{-2} s^{-1}), cautionary notes are necessary. (1) Systematic model errors occur in some instances at low soil water content, for example, at the Èvora site (E), modeled soil respiration was
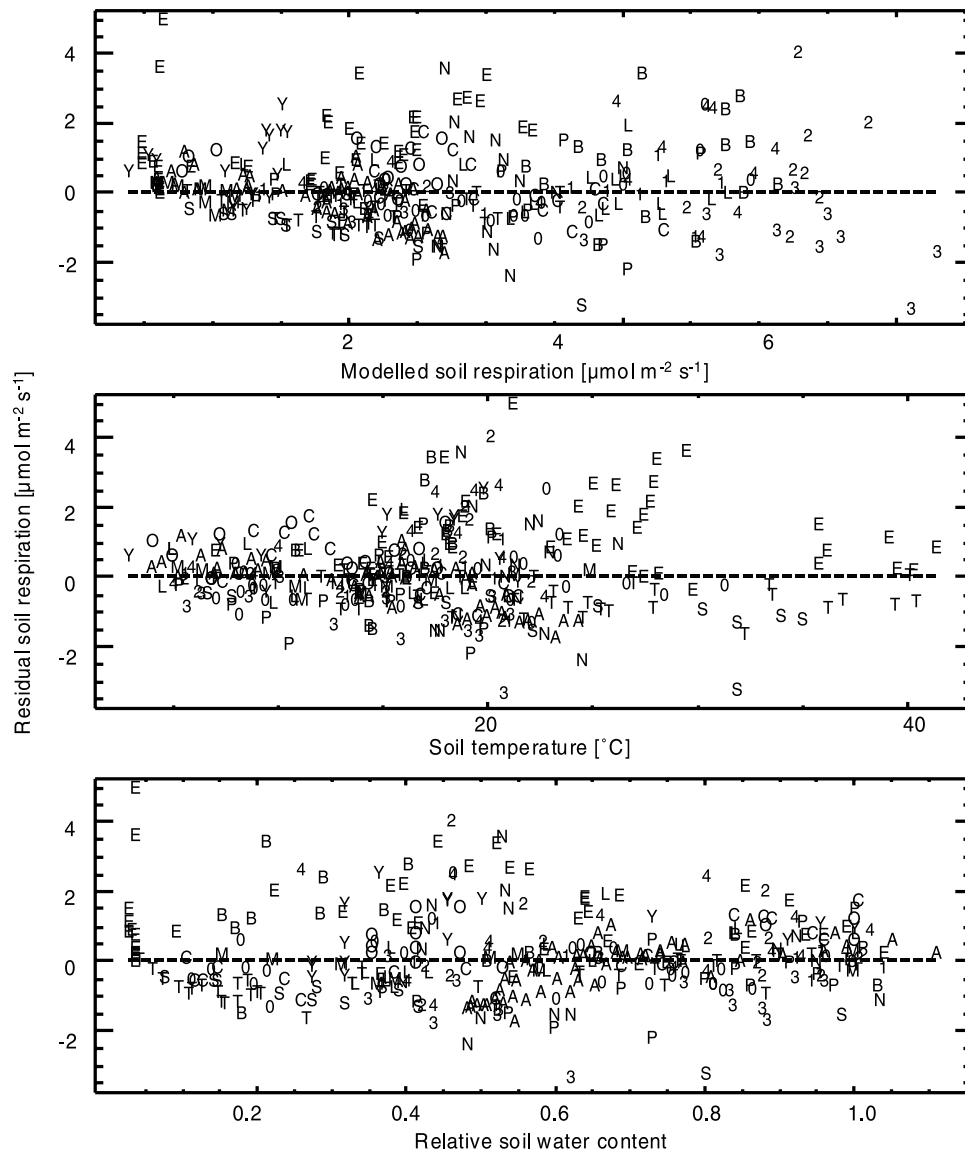

Figure 2. Observed versus modeled soil respiration with the general regression model (see equations (2)–(6); Table 2). Dashed line is the 1:1 line. For site labels, see Table 1. Inset magnifies region from 0 to 3 μmol m^{-2} s^{-1}.

Figure 3. Residual plots for the model (equations (2)–(6)), parameterized after Table 2. Residuals are plotted against modeled soil respiration, soil temperature and relative soil water content. For site labels, see Table 1.

4 to 6 times lower than observed in two cases (Figure 2). These cases correspond to periods when small rain events did not penetrate deeply into the soil, so that they were not detected by TDR sensors. They stress the importance of surface moisture for soil respiration under particular circumstances. Additionally, higher observed than modeled respiration rates in dry soil can signify that respiration still comes from deep soil layers and the root system even when the upper-layer microbes are not active [cf. *Irvine and Law*, 2002]. Indeed, introducing a "baseline" respiration as an additional parameter in equation (2) (respiration independent of temperature and moisture) of 0.89 μmol m^{-2} s^{-1} improved the explained variance by 2% and reduced some of the model bias (not shown). (2) The model cannot account for the effect of episodic rain events that sometimes cause huge respiration rates through stimulation of microbial rapid decomposition (the so-called "Birch-effect"

[*Birch*, 1958; *Orchard and Cook*, 1983]). How important this effect is for monthly and annual carbon balances has to be investigated by continuous observations of soil respiration [e.g., *Subke et al.*, 2003]. (3) One should be cautious when using the model under conditions that did not occur in the current data set, i.e., at very high temperatures combined with high soil water content, where the model predicts respiration rates exceeding 10 μmol m^{-2} s^{-1}. (4) Without further testing, the model is strictly applicable only for similar sites, i.e., temperate to arid forest or shrub-dominated ecosystems.

3.2. Monthly Time Step

[24] On a monthly time step, we were able to test the model proposed by *Raich et al.* [2002], which employed monthly average air temperatures and precipitation sums as predictors for monthly soil respiration rates (hereinafter
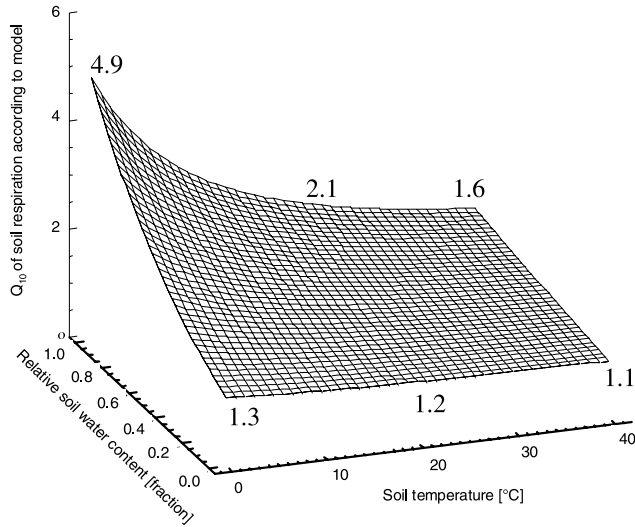
Figure 4. Response surface of the expected Q_{10} of soil respiration as a function of soil temperature and relative extractable water according to the general model (equations (2)–(6)) fitted to the soil respiration data. Indicated are the modeled Q_{10} values at the combinations of 0°, 20°, and 40°C with relative soil water contents of 0.02 and 1.0.

called T&P model). Both with the original and with an optimized parameterization, the model explained less than 25% of the spatial and temporal variation of monthly soil respiration (Figures 5a and 5b, Table 4). One property of the T&P model is the prediction of zero respiration in months without rainfall that is not supported by the data (Figures 5a and 5b). The bias is the result of the fact that the model does not take into account the soil water storage capacity that keeps accumulated precipitation from previous months. This effect can be modeled by simple soil water balance models [*Rambal*, 1993] or via more statistical approaches, for example, by including previous months' respiration as a predictor.

[25] Another fundamental model bias is seen from Figure 6, where average respiration rates per site are plotted. Virtually no intersite variation in soil respiration is explained by the T&P model (Figures 6a and 6b). However, the model residuals are strongly and highly significantly correlated with site peak leaf area index (Figures 6c and 6d), indicating that the latter accounts for the intersite variability that is not explained by the T&P model. Thus the importance of leaf area index as a factor influencing soil respiration as discussed above is also evident from the monthly time step model approach.

[26] The perception of the two model biases in the T&P model (no respiration with zero monthly precipitation and missing LAI effects) led to a new model formulation
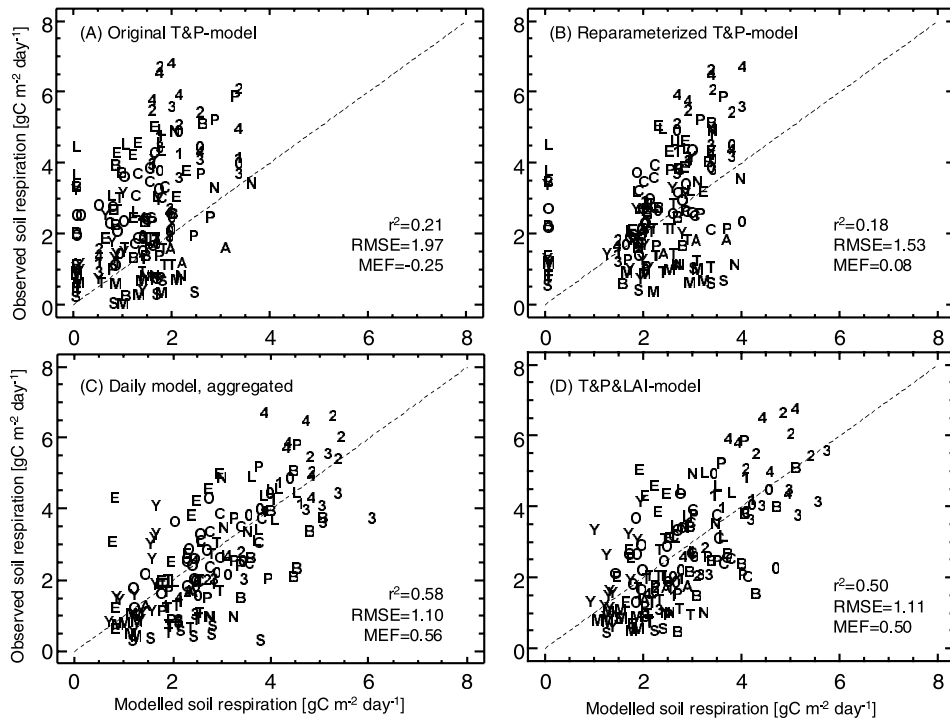

Figure 5. Comparison of monthly observed and modeled soil respiration rates with different models. (a) Original model as by *Raich et al.* [2002] using temperature and precipitation as predictors (T&P model); (b) model as by *Raich et al.* [2002] but with parameters newly fitted to the data; (c) model in this study (equations (2)–(6)), aggregated to monthly values; (d) new model based on that of *Raich et al.* [2002] with inclusion of site peak leaf area index as additional predictor (T&P&LAI model). Dashed line is 1:1 line, site labels are as in Table 1. RMSE, root mean squared error; MEF, modeling efficiency.
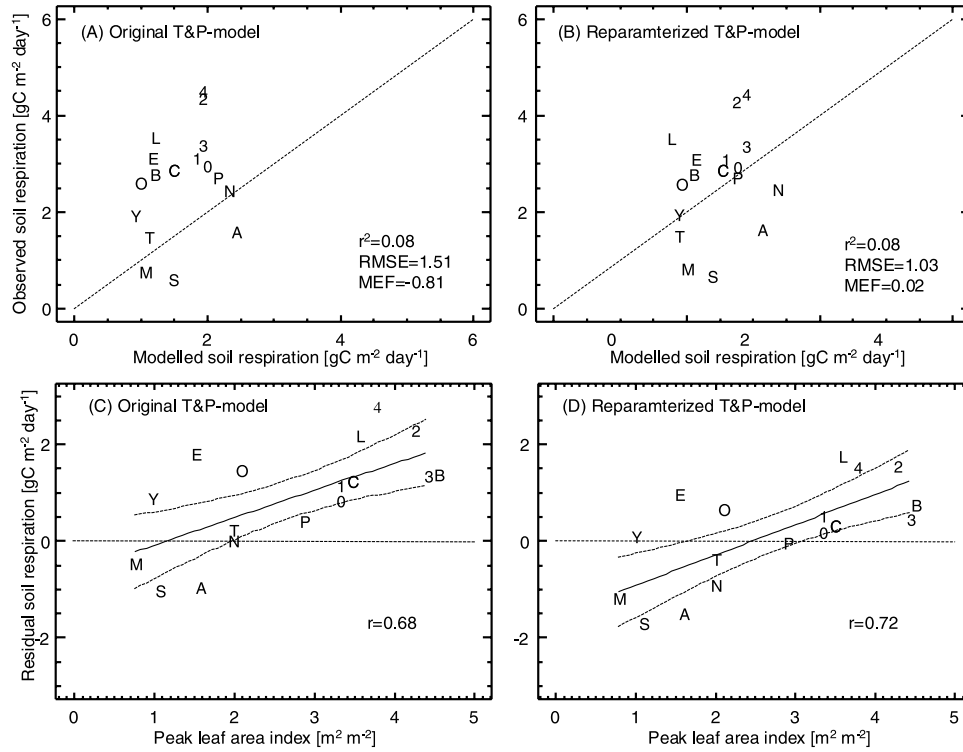
Figure 6. (a, b) Intersite comparison of average observed and modelled soil respiration rates, and (c, d) residual plots versus site peak leaf area index. Figures 6a and 6c give original model as by *Raich et al.* [2002] using temperature and precipitation as predictors (T&P model). Figures 6b and 6d give model as by *Raich et al.* [2002] but with parameters newly fitted to the data. Site labels as in Table 1. RMSE, root mean squared error; MEF, modeling efficiency.

resulting in a model using average monthly air temperature, precipitation sum, and peak site leaf area index as predictors for soil respiration (T&P&LAI model),

$$R_{\text{monthly}} = (R_{\text{LAI}=0} + s_{\text{LAI}} \cdot \text{LAI}) \cdot e^{Q \cdot T_a} \cdot \frac{P + P_0}{K + P + P_0}. \quad (8)$$

[27] In this equation the term $(R_{\text{LAI}=0} + s_{\text{LAI}} \cdot \text{LAI})$ describes a linear dependency of the basal rate of soil respiration (see R_0 in equation (7)) on site peak leaf area index, while Q, T_a, P, and K are as in equation (7). The parameter P_0 is a simple representation of the fact that there can be soil respiration in months without rain, amounting to the fraction $P_0/(K + P_0)$ of non-water limited soil respiration. According to the parameterization of the T&P&LAI model as optimized for the current data set (Table 4), this fraction equals 42%, pointing toward the potential importance of soil water storage. Nevertheless, it is also evident that a simple approach as the T&P&LAI model presented is able to mimic this soil water storage effect, since this model is nearly as successful as the daily time step model that specifically accounts for soil water content (compare Figures 6c and 6d). The parameterization of the T&P&LAI model (Table 4) indicates a much stronger nonlinearity in the response of soil respiration to water deficit compared to the original T&P model, resulting in a strong negative influence on soil respiration when monthly precipitation declines below 20 mm, but with near saturation when precipitation

is above 30 mm (see Figure 7). In contrast, the T&P model shows half-saturation only at 42 mm month^{-1}, and still a 20% reduction at 150 mm month^{-1}. However, when comparing these two parameterizations, one should consider that very likely a background correlation between precipitation, productivity, and soil respiration is confounding the apparent
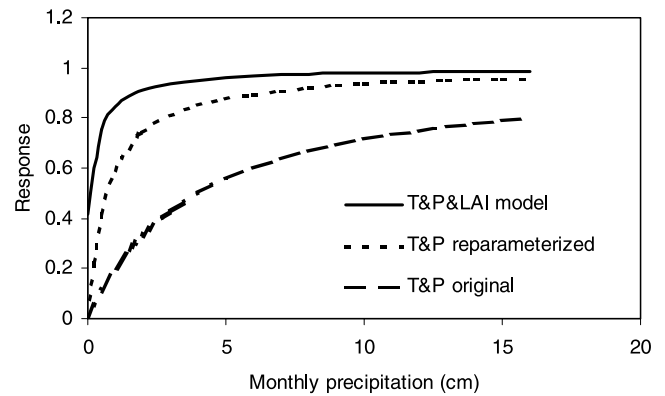

Figure 7. Response function of soil respiration to monthly precipitation according to original T&P model [*Raich et al.*, 2002], reparamerized T&P model, and T&P&LAI model. The parameter estimates in Table 4 were utilized to draw the curves.

Table 3. Correlation Matrix for the Site Variables From Table 1[a]

	R_{ref}	LAI	Leaf Litterfall	Leaf Production	Total C_{soil}	C_{litter}	Aboveground Biomass	Leaf Biomass	Annual Average Precipitation	Drought Index	Annual Air Temperature
R_{ref}		0.83 **	0.77 **	0.74 **	0.30 NS	0.39 NS	0.26 NS	0.47 NS	0.64 **	0.54 *	−0.09 NS
LAI	0.83 **		0.94 **	0.93 **	0.23 NS	0.38 NS	0.33 NS	0.58 *	0.55 *	0.34 NS	0.14 NS
Leaf litterfall	0.79 **	0.96 **		0.90 **	0.24 NS	0.42 NS	0.51 NS	0.63 **	0.42 NS	0.30 NS	−0.09 NS
Leaf production	0.76 **	0.91 **	0.89 **		0.47 NS	0.49 NS	0.25 NS	0.71 **	0.68 **	0.50 *	0.03 NS
Total C_{soil}	0.31 NS	0.28 NS	0.35 NS	0.43 NS		0.51 NS	−0.21 NS	0.52 *	0.69 **	0.70 **	−0.14 NS
C_{litter}	0.51 NS	0.35 NS	0.31 NS	0.35 NS	0.56 NS		0.03 NS	0.24 NS	0.29 NS	0.15 NS	0.02 NS
Aboveground biomass	0.33 NS	0.51 NS	0.62 *	0.45 NS	−0.17 NS	−0.10 NS		0.29 NS	−0.03 NS	0.02 NS	−0.32 NS
Leaf biomass	0.60 *	0.72 **	0.63 *	0.74 **	0.30 NS	0.21 NS	0.30 NS		0.43 NS	0.50 *	−0.27 NS
Annual average precipitation	0.70 **	0.65 **	0.59 *	0.77 **	0.40 NS	0.06 NS	0.24 NS	0.38 NS		0.89 **	−0.12 NS
Drought index	0.64 **	0.46 NS	0.48 NS	0.57 *	0.34 NS	−0.15 NS	0.19 NS	0.36 NS	0.89 **		−0.53 NS
Annual air temperature	−0.25 NS	−0.10 NS	−0.37 NS	−0.29 NS	−0.13 NS	0.00 NS	−0.25 NS	−0.38 NS	−0.21 NS	−0.61 NS	

[a]Product-momentum correlation coefficients are shown in the upper triangle of the matrix; Spearman rank correlation coefficients are shown in the lower triangle. R_{ref} is the regression parameter in equation (2) optimized for each individual site separately. The level of significance is indicated (**:$p < 0.01$; *: $p < 0.05$; NS: $p > 0.05$).

response of respiration to water availability in the T&P model (see Table 3).

[28] Compared to the T&P model the T&P&LAI model explains particularly well the site-to-site variability of soil respiration (Figure 8). The explained intersite variance of around two thirds is only marginally, and in fact not statistically significantly (overlap of bootstrap standard errors), lower than with the daily time step model. In accordance with *Raich and Potter* [1995], this indicates that relatively little information is lost when going from a daily to a monthly time step, and the selection of the most crucial factors as predictors in the model is more important than the selection of the model time step.

3.3. Overall Discussion
3.3.1. Effects of Temperature

[29] Temperature is the most commonly studied environmental control on soil respiration as summarized in a number of reviews [*Singh and Gupta*, 1977; *Raich and Schlesinger*, 1992; *Lloyd and Taylor*, 1994; *Kätterer et al.*, 1998]. All of these studies show that soil respiration increases exponentially with temperature when soil moisture or other factors are not limiting. This direct effect of temperature on soil respiration is often included in models of the global carbon cycle as a constant Q_{10} function [*Hunt et al.*, 1996; *Cox et al.*, 2000]. Nevertheless, there is strong indication that the Q_{10} of respiration declines with increasing temperature [*Lloyd and Taylor*, 1994] and with decreasing water availability [*Carlyle and Bathan*, 1988; *Borken et al.*, 1999; *Reichstein et al.*, 2002a]. Furthermore, there are studies that operate on larger spatial or temporal scales that negate an overall effect of temperature on decomposition or soil respiration [*Liski et al.*, 1999; *Valentini et al.*, 2000; *Giardina and Ryan*, 2000; *Janssens et al.*, 2001]. However, these latter studies use single-factor correlations between temperature and soil respiration, that can easily be confounded by other factors [*Davidson et al.*, 1998]. Thus these studies do not contradict the general positive response of soil respiration to temperature, but indicate that temperature is not necessarily the single most important factor. In this study we were able to partly separate the effects of temperature, moisture availability,
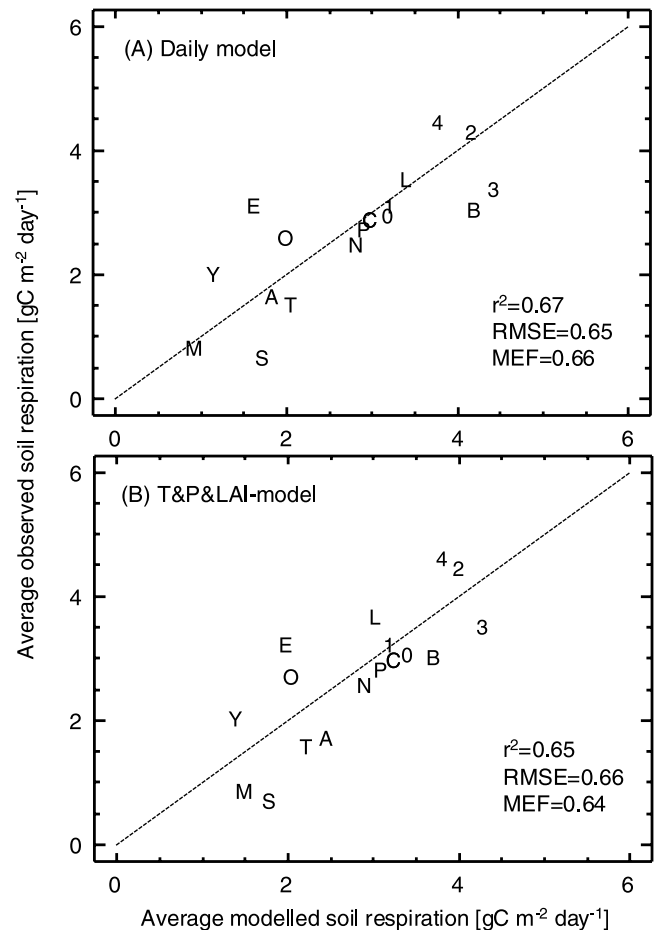

Figure 8. Intersite comparison of average observed and modeled soil respiration rates. (a) Model (equations (2)−(6)) in this study, aggregated to monthly values; (b) new model based on that of *Raich et al.* [2002] with inclusion of site peak leaf area index as additional predictor (T&P&LAI model). Site labels as in Table 1. RMSE, root mean squared error; MEF, modeling efficiency.

Table 4. Regression Parameters and Statistics for the T&P and T&P&LAI Models Operating on a Monthly Time Step[a]

| Model | Parameters | | | | | | Statistics | |
	$R_{LAI = 0}$, gC m^{-2} day^{-1}	s_{LAI}, gC m^{-2} day^{-1}	R_0, gC m^{-2} day^{-1}	Q, °C^{-1}	K, cm	P_0, cm	RMSE, gC m^{-2} day^{-1}	r^2
T&P model original	NA	NA	1.25	0.05452	4.259	NA	1.57	0.21
T&P model reparameterized	NA	NA	1.31 [0.94, 1.88]	0.0485 [0.022, 0.066]	0.2295 [0.096, 0.363]	NA	1.53	0.18
T&P&LAI-model (all data)	0.48 [0.27, 0.68]	0.31 [0.18, 0.36]	NA	0.03918 [0.027, 0.055]	0.215 [0.05, 0.29]	0.155 [0.02, 0.25]	1.11	0.50
T&P&LAI model (NaOH-method, site Maials excluded)	0.55 [0.33, 0.76]	0.30 [0.17, 0.36]	NA	0.04122 [0.028, 0.057]	0.210 [0.05, 0.29]	0.149 [0.017, 0.26]	1.13	0.48

[a]The (asymmetric) 90% confidence intervals from the bootstrap estimation are depicted in brackets, where applicable. The parameters are defined in equations (7) and (8). NA, not applicable.

and vegetation productivity on soil respiration and show that all effects are important in determining the spatiotemporal pattern of soil respiration through an interaction that can be captured by a model as in the current study. With respect to the temperature dependence, the daily time step analysis confirms a general positive response of soil respiration to temperature, but questions the invariability of the temperature sensitivity (Q_{10}) as assumed in most models [*Hunt et al.*, 1996; *Rodrigo et al.*, 1997; *Cox et al.*, 2000]. Instead, the model parameterization indicates in nonlinear dependency of the Q_{10} on soil moisture and temperature. A decreased temperature sensitivity under dry conditions may mitigate the positive feedback that soils presumably exert on global warming.

3.3.2. Effects of Moisture

[30] In general, three phases of the response of soil respiration to soil moisture can be identified: (1) When soils are relatively dry, metabolic activity increases strongly with water availability [*Howard and Howard*, 1993]; (2) there is a broad range of near optimum soil water content where changes in soil moisture only have little effect, if any, on soil respiration [*Scheffer and Schachtschabel*, 1992]; and (3) above field capacity and toward saturation, oxygen deficiencies inhibit aerobic respiration [*Skopp et al.*, 1990]. Here we included only the first two phases into the model since all sites were well drained during the observation periods. The effect of soil moisture on soil respiration has been incorporated differently in the daily and monthly time step model. With the daily time step model the actual soil moisture could be directly used as a predictor, and the relative soil water content of the upper soil layer as a fraction of field capacity proved to be a good indicator of water availability. The conceptual weakness of the monthly time step models is that monthly precipitation was taken as a surrogate for soil moisture, while the actual soil water availability also depends on soil water storage capacity, the water balance during previous weeks and months, and the rainfall distribution within the month. For instance, on several sites, there is considerable soil respiration, even in months without precipitation, that is not captured by the T&P model, which assumes no soil respiration with no precipitation (Figure 5). This bias can be avoided by means of a simple water balance model that computes month-to-month variations of soil water storage. A similar approach

has been taken for predicting monthly gross ecosystem production at FLUXNET sites [*Law et al.*, 2002]. However, this approach needs input data like soil field capacity or evapotranspiration rates that are still uncertain at large spatial scales. Here we used a simpler empirical approach in the monthly step T&P&LAI model and introduced a parameter (P_0) that shifts the hyperbolic relationship between precipitation and soil respiration that is implemented in the T&P model. Despite its simplicity, this approach avoids the bias of the ''zero-precipitation-zero-respiration'' assumption and yields results that were statistically indistinguishable from the much more detailed daily time step approach. The parameterization of this model (Table 4, Figure 7) indicates that on average a soil respiration of 40% of maximal (not water-limited) soil respiration can be maintained in months of zero precipitation. This result obviously stresses the importance of soil water storage for soil respiration for the sites studied here and points out the capacity of forest soils to hold relatively high biological activity even at low water supply.

3.3.3. Effects of Vegetation

[31] Vegetation influences soil respiration through multiple pathways: (1) Through interception of radiation energy and modification of the land-surface roughness, vegetation changes the energy balance of the soil [*Jones*, 1996; *Raich and Tufekcioglu*, 2000]. (2) Through interception of precipitation and extraction of soil water via transpiration vegetation alters the soil moisture regime [e.g., *Rutter and Morton*, 1977]. (3) Dead plant material [*Gillon et al.*, 1999] provides the principal carbon source to microorganisms. Both the litter quality and the amount of litter determine the amount of litter respired as CO_2 [*Swift et al.*, 1979]. (4) A considerable fraction, (10-)30−70(−90)% [cf. *Hanson et al.*, 2000], of soil respiration directly stems from the vegetation via root or rhizosphere respiration.

[32] In some instances the influence of vegetation on soil microclimate has been shown to be sufficient to explain differences of soil respiration rates between different vegetation types [*Raich and Tufekcioglu*, 2000]. However, a number of recent studies at different scales is indicating that the input of carbon through primary productivity is driving soil respiration to a large extent [*Hogberg et al.*, 2001]. The obvious intercorrelation between climate variables, net primary productivity, and soil respiration has led to some

controversy in the past about which factors are driving the differences of soil respiration between different sites. While *Raich and Schlesinger* [1992] found strong correlation between net primary productivity and soil respiration when comparing different biome types, they argue that this correlation is mainly caused by a background correlation of both quantities with climate variables [e.g., *Raich and Tufekcioglu*, 2000]. On the contrary, other studies argue for a direct effect of vegetation productivity on soil respiration that can overrule climatic influences [*Valentini et al.*, 2000; *Janssens et al.*, 2001]. In the current study, we were able to separate the direct climate and the vegetation effects by first correcting the soil respiration data for temperature and moisture influences resulting in standardized (18°C, without water limitation) site-specific respiration rates. These standardized respiration data were strongly correlated with indices of vegetation productivity like leaf production or leaf area index, clearly indicating that both climate and vegetation are important (direct and indirect) contributors to the spatial variability of soil respiration at a global scale.

3.3.4. Model Improvements and Limitations

[33] Both the daily time step model (equations (2)–(6)) and the monthly T&P&LAI model (equation (8)) account for these partly independent effects of climate and vegetation. Thus, they are expected to account for that part of variability in soil respiration that is not caused by climate but by other constraints like soil properties, management, and disturbance. For instance, the Yatir and the Maials sites are climatically similar and are hardly distinguished by the climate-driven model. However, since the Yatir site is more productive than the Maials site due to better pedological conditions, there is variability between the sites that is captured by the models that employing leaf area index. Similarly, the variability within the chronosequences of the data set (Y, O, and 0–4) is much better captured by the models that include the variation in leaf area index into the model. Nevertheless, major limitations of the T&P&LAI model should be noted. The linear relationship between standardized soil respiration and leaf area index that was valid in the current study for leaf area indices up to 4.8 is unlikely to persist toward higher leaf area indices and a saturation response is to be expected, particularly in high-latitude coniferous forests. Assuming as a first approximation that productivity is proportional to the absorbed radiation and that soil respiration is proportional to site productivity, an exponential relationship of the form $R_{ref} = R_{ref,\ max} \cdot (1 - e^{-k \cdot LAI})$ may be expected. However, this simple relationship will be confounded by that fact that productivity is often limited by other factors than available radiation (drought, nutrient availability, temperature constraints). Certainly, the strongest limitation of this simple and empirical T&P&LAI model is that it is not dynamic; that is, effects of site history and lag effects in decomposition dynamics cannot be accounted for. For instance, a clear-cut site will develop a low leaf area index during the first year, but contain large amounts of fresh organic matter in form of litter and dead roots that trigger a higher soil respiration than expected by the empirical model. This problem can only be tackled by use of a dynamic decomposition model [*Parton et al.*, 1987]. However, dynamics

decomposition models suffer from the fact that they may only be parameterized globally via a number of difficult assumptions, and that they have to rely on century-spanning "spin-up runs" to equilibrate the soil carbon pools without being able to account for long-term climate fluctuations and land-use change. A worthwhile further step in continental to global respiration modeling will be to analyze whether dynamic ecosystem models are able to capture the pattern of soil respiration found in this study.

3.3.5. Modeling Soil Respiration at a Continental to Global Scale

[34] In the past decade, quite different approaches have been taken in the global analyses of soil respiration. On the one hand, there are a number of mechanistically based models [*Schimel et al.*, 1997; *Parton et al.*, 1998; *Cramer et al.*, 1999; *Schimel et al.*, 2000; *Cramer et al.*, 2001] that aim at providing a theoretical process level basis for understanding and analyzing the effects of environmental change on ecosystem carbon fluxes. There is a great need to validate those mechanistic models, which is not an easy task [*Rastetter et al.*, 1992]. While model intercomparison is an important tool, it is limited since different models are not independent because they often rely on similar theory (e.g., first-order reaction kinetics) and data [cf. *Cramer et al.*, 1999]. Thus, on the other hand, simple statistical models that aim at summarizing current data and at extracting general trends are important as an independent means for validation of the more complex mechanistic models. In the context of the current study, this means it is worthwhile testing whether current mechanistic models show the drought-dependent variable temperature sensitivity of soil respiration (e.g., as the result of a differential response of autotrophic and heterotrophic respiration) and whether they predict a close correlation between soil respiration and leaf area index as observed in the current study.

[35] By definition, a statistical model only reflects the statistical influence of different factors but does not explain the underlying reasons for the influence. Nevertheless, such a model should still incorporate the most important factors in order to avoid relationships that are confounded by background correlations [*Draper and Smith*, 1981]. The T&P&LAI model introduced here has got the advantage over purely climate-driven models since it accounts for important biological variation in soil respiration, while still being much simpler and easier to apply than mechanistically based models. The inclusion of leaf area index as an integrative predictor has got a plausible mechanistic basis (being a surrogate of site productivity and carbon input into the soil), and moreover provides compatibility with remote sensing approaches that are currently used for the estimation of gross and net primary productivity (GPP, NPP [e.g., *Potter et al.*, 1993; S. W. Running et al., MODIS Daily Photosynthesis (PSN) and Annual Net Primary Production (Npp) Product (MOD17), Algorithm Theoretical Basis Document, Version 3.0, 1999, available at http://www.ntsg.umt.edu/modis/ATBD/ATBD_MOD17_v21.pdf] (hereinafter referred to as Running et al., database, 1999)). In fact, the T&P&LAI model could directly link into the MODIS-GPP/NPP data stream that is currently the only globally operational system with near real-time calculation

of GPP and NPP (Running et al., database, 1999), where only precipitation as an additional variable would be required. However, as mentioned above, an evaluation of this model in the tropical, cold-temperate and boreal biomes is necessary before applying it at global scale.

4. Conclusions

[36] In conclusion, this study reinforces the importance of drought effects on soil respiration and extends previous findings that the temperature sensitivity of ecosystem respiration is not constant with changing soil water availability to measured soil respiration at a large number of sites affected by drought. These drought effects will diminish the positive feedback of soils CO_2 emissions to global warming. Furthermore, we show that biological variability is important for predicting spatial variability of soil respiration at continental to global scales in a way that cannot be explained by climate alone. However, the biological variability can still be captured by a simple model that is easily applicable at large scales and that includes leaf area index as an integrative variable, thus providing a strong potential link to remote sensing. We expect significant improvements of soil respiration predictions for locations where other factors than climate limit net primary productivity and soil respiration.

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