12 Climatic Influences on Seasonal and Spatial Differences in Soil CO_2 Efflux

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12.1 Modeling the Temporal Variability of Soil CO_2 Efflux

The efflux of CO_2 from the soil is characterized by large seasonal fluctuations due to seasonal changes in root and microbial respiration. Although several biotic and abiotic factors influence root and microbial activity (see Chap. 3), the control exerted by temperature, and in some cases moisture, is usually dominant. In the absence of water stress, variation in soil temperature accounts for most of the seasonal and diurnal variation in soil CO_2 efflux. Where water stress frequently occurs, soil CO_2 efflux may not be correlated with soil temperature, but with its moisture content (Rout and Gupta 1989). Thus, CO_2 release from the soil appears to respond to temperature or moisture, whichever is most limiting at the time of measurement (Schlentner and van Cleve 1985).

Interest in the rate-controlling factors of soil CO_2 efflux is growing because of the potential for climate change to increase the flux of CO_2 from the ecosystems to the atmosphere (Raich and Potter 1995). Information on the relationship between soil CO_2 efflux and its driving variables is also needed for the development of models of value for the assessment of climate-change effects and for the interpretation of the processes involved.

Soil CO_2 efflux has been successfully modeled with process-based models that simulate root and microbial respiration separately (Simunek and Suarez 1993; Freijer and Leffelaar 1996; Fang and Moncrieff 1999). These one-dimensional models use Fick's diffusion law to describe the transport of CO_2 in soil, dependent on soil characteristics, soil water content, and temperature. However, because soil CO_2 efflux can be successfully modeled using only the temperature and moisture relationships (Keith et al. 1997; Epron et al. 1999a; Janssens et al. 1999; Buchmann 2000; Longdoz et al. 2000), empirical models are most frequently used to simulate soil CO_2 efflux.

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12.1.1 Temperature Responses

Microbial communities and plant root systems are particularly sensitive to changes in soil temperature (Killham 1994). Both specific respiration rates and microbial and root biomass are positively affected by elevated temperature, and in most ecosystems a positive correlation between soil CO_2 efflux and temperature is observed (Singh and Gupta 1977), leading to large seasonal fluctuations in the flux rates. This positive relationship between soil CO_2 efflux and temperature was also observed in most of the EUROFLUX forests.

There is, however, no consensus on the exact form of the relationship (Lloyd and Taylor 1994). Soil CO_2 efflux has been modeled using linear (Witkamp 1966; Anderson 1973), power (Kucera and Kirkham 1971), and sigmoid (Schlentner and van Cleve 1985; Janssens et al. 1999; Matteucci et al. 2000) relationships with temperature (Table 12.1). However, exponential rela-

Table 12.1. List of relationships between soil CO_2 efflux and soil temperature that have been applied in empirical models

Relationship	Equation[a]	Comments
Linear	$SR = a + b \times Temp$	
Power function	$SR = a \times Temp^{b}$	
Sigmoid	$SR = a + \left(\frac{1}{b + c\left(\frac{10 - Temp}{10}\right)}\right)$	
Exponential	$SR = a \times e^{b \times Temp}$	
Q_{10} function	$SR = SR_{ref} \times Q_{10}\left(\frac{Temp - Temp_{ref}}{10}\right)$	
Arrhenius type	$SR = SR_{10} \times e\left(Ea \times \left(\frac{Temp - 283.15}{283.15 \times Temp \times R_g}\right)\right)$	Temp in K R_g = gas constant = 8.314 J mol^{-1} K^{-1} Ea = Activation Energy $\left(J\ mol^{-1}\right) = a \times \left(\frac{Temp}{Temp - 227.13}\right)$

[a] SR, soil CO_2 efflux; $Temp$, soil temperature; SR_{ref}, soil CO_2 efflux at reference temperature; $Temp_{ref}$, reference temperature; SR_{10}, soil CO_2 efflux at 10 °C; a, b, and c are constants.

tionships, especially the Q_{10} relationship, are more frequently used to predict respiration rates from temperature (Peterjohn et al. 1994; Raich and Potter 1995; Boone et al. 1998; Davidson et al. 1998; Epron et al. 1999a; Buchmann 2000; Morén and Lindroth 2000).

The median value of the reported Q_{10} values for forest soil CO_2 efflux is 2.4, but the range is very broad (Schleser 1982; Raich and Schlesinger 1992; Kicklighter et al. 1994; Kirschbaum 1995). The use of the Q_{10} relationship often has been criticized because the Q_{10} factor itself decreases with increasing temperature and depends on soil moisture conditions (Howard and Howard 1993). This problem may be mitigated by using a temperature-dependent (McGuire et al. 1992) or a moisture-dependent Q_{10} factor (Carlyle and Than 1988). However, Lloyd and Taylor (1994) reported that the assumption of an exponential Q_{10} relation between soil respiration and soil temperature is invalid and systematically leads to underestimated fluxes at low temperatures, and overestimated fluxes at high temperatures. They found that soil respiration was better described by an Arrhenius-type relationship in which the activation energy decreases with increasing soil temperature.

12.1.2 Sensitivity of Empirical Models to the Type of Temperature Regression

To test the use of different temperature response functions, we fitted three of the equations listed in Table 12.1 (i.e., Q_{10}, Arrhenius, and sigmoid) to data from the BE-2 site (Table 12.2). With the parameterized temperature response functions we then simulated soil CO_2 efflux from the measured soil temperatures (Fig. 12.1).

In general, all regressions fitted the data well (Table 12.2, Fig. 12.1). Although the different regressions did not result in significant differences in the total annual soil CO_2 efflux (Table 12.2), we observed large deviations during the year. In mid-summer, when soil temperature exceeded the temperature range observed during the fitting exercise, the Arrhenius and Q_{10} relationships produced significantly higher estimates of soil CO_2 efflux than the sigmoid relationship (Fig. 12.1). At temperatures below 5 °C the opposite was observed. These differences highlight the importance of measuring soil CO_2 efflux in the widest possible temperature range in order to obtain an optimal parameterization of the models. However, high soil temperature often coincides with low moisture availability, confounding the temperature response of soil CO_2 efflux. Therefore, it may be difficult to get the necessary data, especially at drier sites, and an irrigation experiment during warm, drought-stressed periods could be very informative.

The sigmoid response function provided the best fit at the BE-2 site. However, this was not the case at other sites. At the FR-1 site, the sigmoid function showed the weakest fit with the data, and at the GE-1 site an exponential func-

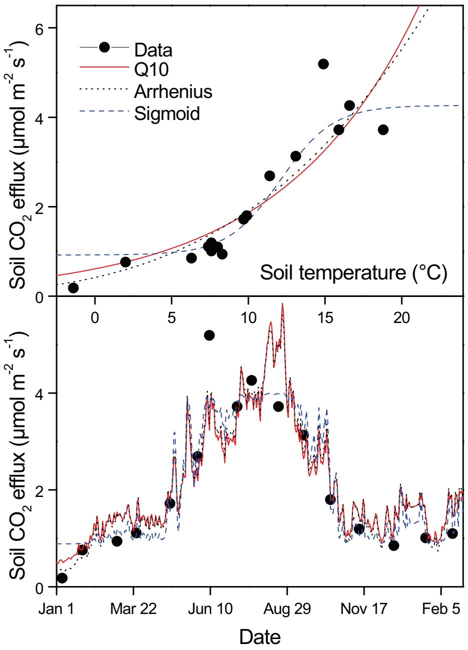

Fig. 12.1. *Top panel* Plot of the temperature response functions (fitted to the data from the BE-2 oak site) that were applied to simulate the annual soil CO_2 efflux rates in Table 12.2. Soil temperature was measured at 5 cm. *Bottom panel* Time series of the measured and simulated soil CO_2 efflux rates in the BE-2 oak site. Regressions and parameters are given in Tables 12.1 and 12.2. Data shown are for 1997 and the beginning of 1998

Table 12.2. List of the regressions that were fitted to the data from the BE-2 site and the obtained parameter values. Regressions are listed in Table 12.1. Total annual flux is in g C m^{-2} $year^{-1}$, range is in µmol CO_2 m^{-2} s^{-1}, R2adj is adjusted R^2

Regression	Parameter values	Total annual flux	Range	R2adj	*n*
Q_{10}	SR_{ref}=1.87, Q_{10}=2.87	825	0.47–5.85	0.685	23
Arrhenius	SR_{10}=1.91, a=1.65×10^4	820	0.27–5.37	0.732	23
Sigmoid	a=0.888, b=0.320, c=891	819	0.89–4.00	0.832	23

tion was found to fit the measured fluxes best. Whichever model is selected to simulate soil CO_2 efflux from soil temperature, the annual totals are not likely to differ significantly. However, inappropriate models may introduce significant errors in the estimated fluxes during the year.

12.1.3 Moisture Responses

Soil moisture may negatively affect soil CO_2 efflux rates when it becomes either very high (poor aeration and reduced CO_2 diffusivity) or too low (desiccation stress). In drought-stressed ecosystems, soil CO_2 efflux usually peaks in spring and after rain events (Matteucci et al. 2000). Soil temperature is often poorly correlated with soil CO_2 efflux (Fig. 12.2), and soil moisture may become the best predictor of soil CO_2 efflux (Rout and Gupta 1989; Holt et al. 1990; Keith et al. 1997).

The shape of the moisture response curve and the moisture content at which maximum respiration occurs depend on an array of site-specific factors such as soil texture and structure, amount and type of organic matter, and soil temperature (Howard and Howard 1993). Nonetheless, the response of soil CO_2 efflux to soil moisture has been successfully described using linear (Kowalenko et al. 1978; Rout and Gupta 1989; Holt et al. 1990; Epron et al. 1999a), exponential (Keith et al. 1997; Davidson et al. 1998), power (Skopp et al. 1990), Gompertz (Janssens et al. 1999), and first- (Hanson et al. 1993), and second-degree inverse polynomial functions (Bunnell et al. 1977; Schlentner and van Cleve 1985; Carlyle and Than 1988; Table 12.3).

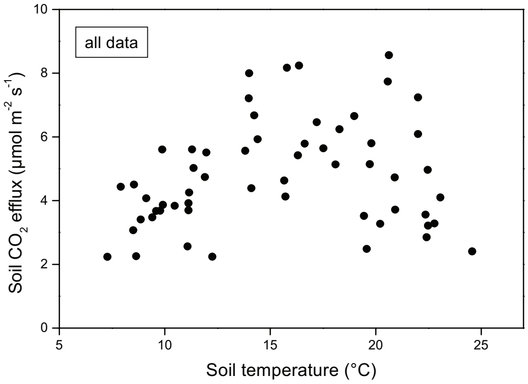

Fig. 12.2. The temperature relationship of soil CO_2 efflux in the IT-2 site. Soil temperature was measured at 5 cm depth

Table 12.3. List of moisture response functions of soil CO_2 efflux that have been applied in empirical models. *f*(M) = moisture response function, M = moisture content, and a, b, and c are constants

Relationship	Equation	Comments
Linear	$f(M)=a+b \times M$	
Exponential	$f(M)=a \times e^{b \times M}$	
Power	$f(M)=a \times M^{b}$	
Gompertz function	$f(M)=e^{-e^{(a-b \times M}}$	
First-degree inverse polynomial		
Second-degree inverse polynomial		
	a=M at half field capacity	
		b=M at half water
holding capacity		
		c=scaling factor

12.1.4 Sensitivity of Empirical Models to the Type of Moisture Regression

We selected the IT-2 site to test a number of models for simulating the moisture dependence, because this was the driest of the EUROFLUX sites and soil CO_2 efflux was not correlated with soil temperature (Fig. 12.2). Thus, variability in the flux simulations from different moisture regressions were expected to be large at this site.

First, a Q_{10} temperature relation was derived, using data that were not limited by soil moisture, i.e., when soil moisture was above 10 vol% (Fig. 12.3, top panel). With the obtained Q_{10} function we then normalized all data for the influence of temperature and examined the dependence on soil moisture (Fig. 12.3, bottom panel). The normalized data can easily be separated into two groups: above a volumetric moisture content of 10 % (solid circles in Fig. 12.3) they appear to be uncorrelated with moisture, while below that threshold (open circles) a strong correlation is observed.

To test different moisture response curves, we fitted four of the equations listed in Table 12.3 (i.e., linear, Gompertz, and first- and second-degree inverse polynomials) to the data normalized for temperature (Fig. 12.3, Table 12.4). Except for the linear function, all regressions had similar shapes and they all fitted the normalized data rather well. Thus, as long as the mois-

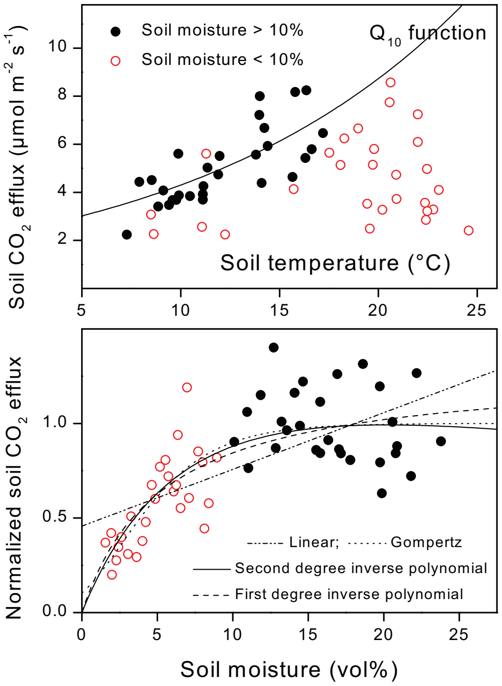

Fig. 12.3. *Top panel* Temperature relationship of soil CO_2 efflux in the IT-2 site. The Q10 function (*solid line*) was fitted to the data without water stress (*solid circles*, soil moisture above 10 vol%). Soil temperature was measured at a 5 cm depth. *Bottom panel* Plot of the moisture response functions and the normalized soil fluxes versus soil moisture at the IT-2 site. The moisture regressions and parameterization are given in Tables 12.3 and 12.4. Soil moisture was measured in the upper 15 cm with a TRIME system (IMKO GmbH, Germany)

Table 12.4. List of the regressions that were fitted to the data from the IT-2 site and the obtained parameter values. Regressions are listed in Table 12.3. R^2adj is adjusted R^2

Regression	Parameter values	R2adj	*n*
Linear	a=0.457, b=0.03	0.425	56
Gompertz	a=0.824, b=0.308	0.612	56
First-degree inverse polynomial	a=0.244, b=1.29	0.597	56
Second-degree inverse polynomial	a=20.2, b=20.2, c=3.97	0.601	56

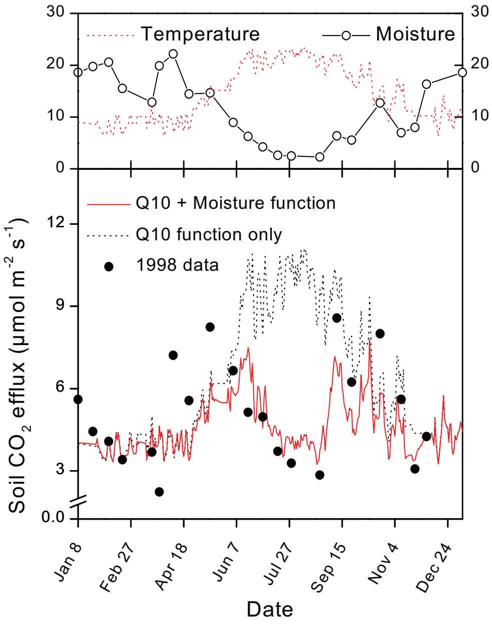

Fig. 12.4. *Top panel* Time series (1997) of mean daily soil temperature and soil moisture at the IT-2 site. Soil temperature was measured at 5 cm, soil moisture in upper 15 cm. *Bottom panel* Time series (1997) of the measured and simulated soil CO_2 efflux rates at the IT-2 site. The Q_{10} function is given in Fig. 12.3. The moisture regression applied in this simulation was a first-degree inverse polynomial (see Tables 12.3 and 12.4 for equation and parameter values)

ture response functions accurately fit the data below the threshold where moisture stress occurs, and approximate the data above that threshold, no significant deviations in the simulated fluxes are to be expected.

As in most drought-stressed ecosystems, soil CO_2 efflux at the IT-2 site peaked in spring and autumn, was low in winter because of moderate temperatures, and diminished (in comparison with spring and autumn) in summer when drought occurred (Fig. 12.4). The Q_{10} function alone [$SR=4.3 \times 2.03^{(Temp-10/10)}$] significantly overestimated soil CO_2 efflux in dry periods. When including a moisture response function (first degree inverse polynomial, see Table 12.4), the empirical model fitted the data better and explained about 60 % of the temporal variability (R^2=0.579, *P*=0.006, *n*=21).

Because predictions of soil CO_2 efflux based solely on temperature do not account for reductions due to moisture limitation, they are likely to overestimate soil CO_2 efflux when drought occurs. At the IT-2 site, the reduction in total annual soil CO_2 efflux induced by drought was 26 % (Fig. 12.4).

Even in forests with less pronounced drought stress, where drought occurs infrequently or moderately, the inclusion of moisture regressions in empirical models will increase their fit with the data. Moderate drought may also partly explain the inter-annual variability in soil CO_2 efflux (Epron et al. 1999a).

12.1.5 Additional Comments on Empirical Models

Empirical models based on soil temperature and moisture usually explain about 60–90 % of the temporal variability in soil CO_2 efflux. The unexplained variability may be due to several factors. For instance, the annual pattern of above- and belowground litterfall may not coincide with that of temperature. Rapid decomposition of the labile components of this fresh litter may thus confound the climate dependency of soil CO_2 efflux (Trumbore et al. 1996).

Some of the variability might also be related to the seasonal changes in the basal rates and temperature sensitivity (Q_{10} coefficient) of respiration that have been observed in forests (Hagihara and Hozumi 1991; Goulden and Crill 1997; Lavigne et al. 1997). Temporal changes in the basal ecosystem respiration rates may be due to the fluctuating root and microbial biomass. Although root production in most tree species in temperate climates is related to soil temperature, root growth often peaks in early summer and diminishes in midsummer due to unfavorable moisture conditions (Lyr and Hoffmann 1967). Also, microbial biomass may vary considerably during the year, usually peaking in spring or summer (Wardle 1998). The annual pattern of root and microbial biomass might therefore be unrelated to that of soil temperature, and increase the scatter in the relationship between soil CO_2 efflux and temperature, thus reducing the predictive power of the empirical models. In addition, roots and microbes may have different temperature sensitivities; temporal decoupling of root and microbial processes might therefore enhance the variability in the temperature response of soil CO_2 efflux.

Another source of unexplained variability in the temperature response may be related to the temperature profile within the soil. Whereas the soil temperature measurements used in the models (usually in the upper soil layers) are coupled to air temperature, temperatures lower in the soil (0.5 m) are not. Although most respiratory activity occurs in the upper soil layers, forests may have significant CO_2 production in the deeper layers (Trumbore et al. 1995). Respiration occurring farther down in the soil will thus be poorly correlated with the near-surface temperature, and confound the temperature response of soil CO_2 efflux.

Besides the natural phenomena mentioned above, an inappropriate measurement depth of soil temperature may also add to the unexplained temporal variability in soil CO_2 efflux. If the measurement depth is too deep (if most respiratory activity occurs above it) then soil temperature will lag behind soil CO_2 efflux, on both a daily and an annual time scale. If the measurement depth is too close to the surface, the opposite will be observed. As a result of this time lag, hysteresis will occur when plotting the complete diurnal or annual cycle of soil CO_2 efflux versus soil temperature: morning (or spring) fluxes will differ from the evening (or fall) fluxes at the same temperature (Janssens et al. 1998). Inappropriate measurement depths will therefore artificially increase the variability in the relationship between the measurements of soil CO_2 efflux and temperature.

To cover the widest possible temperature range, most empirical models are based on in situ measurements of soil CO_2 efflux from all seasons. At this large time scale, respiration is affected not only by temperature and moisture, but also by the changing size of the root and microbial biomass. Thus, when applied to simulate diurnal fluctuations, empirical models using data obtained in both winter and summer may overestimate diurnal fluctuations, because daily changes in root and microbial biomass are much smaller than seasonal changes. This problem may be overcome by smoothing either the model inputs or the outputs over longer time periods. The proper smoothing period will vary from site to site, but can be retrieved by fitting the model simulations to the diurnal patterns of soil CO_2 efflux (Janssens et al. 2001a).

12.2 Spatial Variability Among the EUROFLUX Forests

Large differences in total annual soil CO_2 efflux were observed among the different EUROFLUX forests (Table 12.5). As was shown in the previous section, the use of different temperature and moisture regressions to simulate these fluxes does not contribute to these differences. However, no standard methodology for measuring soil CO_2 efflux was applied in the EUROFLUX network (see Chap. 3). Different methodologies typically result in different fluxes (Norman et al. 1997; Le Dantec et al. 1999; Janssens et al. 2000), and the reader should bear in mind that this lack of standardization is likely to have contributed to the variability found in most of the relationships with the influencing biotic and abiotic factors. None the less, most of the spatial variability in soil CO_2 efflux is likely to be related to differences in climate, vegetation, and site characteristics.

A positive trend was observed in the correlation between soil CO_2 efflux and soil pH, while higher litter layer C/N ratios tended to have a negative

Table 12.5. Overview of soil CO_2 efflux rates and a number of related fluxes and site characteristics in the EUROFLUX sites. TSR = Total annual soil C efflux (g C m^{-2} $year^{-1}$); SR_{10} = soil CO_2 efflux at 10 °C in µmol m^{-2} s^{-1} (for IT1 and IT2 in the absence of drought stress); Tsoil = mean annual soil temperature, at or near a depth of 5 cm (°C); Precip = total annual precipitation (mm); pHsoil = pH_{KCl} of upper mineral soil; TSC = total soil C content (kg C m^{-2}); C/Nlit = C/N ratio of litter layer; TER = total annual ecosystem respiration (g C m^{-2} $year^{-1}$); NPP = aboveground net primary productivity (g C m^{-2} $year^{-1}$)

Site+year	Code	TSR	SR_{10}	Q_{10}	Tsoil	Precip	pHsoil	TSC	C/Nlit	TER	NPP
IT1-(1996–1997)	X	879	4.1	2.2	2.5	1180	5.6	22.7	20.7	636	312
IT2-(1997)	Y	1456	4.3	2.0	14.5	–	5.8	–	–	–	793
ITex-(1998)	A	1379	4.9	3.4	4.0	–	4.4	–	20.7	–	995
BE1Douglas-(1997)	B1	–	1.4	3.0	8.1	792	–	–	–	–	–
BE1beech-(1997)	B2	844	2.6	2.4	8.1	792	–	–	–	1095	–
BE2pine1-(1997)	C1	281	0.7	2.6	10.6	662	2.6	14.4	27.1	–	–
BE2pine2-(1997)	C2	338	0.8	2.4	10.6	662	2.7	14.9	25.3	–	–
BE2oak1-(1997)	C3	578	1.2	3.6	10.6	662	2.6	–	21.3	–	–
BE2oak2-(1997)	C4	769	1.9	3.1	10.6	662	3.5	–	19.6	–	–
FR1-(1996)	F1	509	1.6	3.4	9.1	672	4.8	–	13.4	793	402
FR1-(1997)	F2	685	1.8	3.8	9.6	871	4.8	–	13.4	988	556
FR1-(1998)	F3	713	2.2	4.0	9.4	–	4.8	–	13.4	1235	364
DK-(1996)	D1	370	1.3	6.3	5.8	–	4.4	19.6	17.5	967	–
DK-(1997)	D2	460	1.3	2.8	9.1	510	4.4	19.6	17.5	1107	–
DK-(1998)	D3	–	1.7	5.0	7.4	–	4.4	19.6	17.5	–	–
GE1–47y-(1998)	G1	709	2.4	2.4	6.1	–	3.6	–	22.0	1373	1060
GE1–87y-(1998)	G2	740	2.6	3.2	6.1	–	–	–	–	–	–
GE1–111y-(1998)	G3	859	3.0	2.9	6.1	–	–	–	–	–	–
GE1–146y-(1998)	G4	624	2.1	2.4	6.1	–	–	–	–	–	534
GE-Kiel-(1997)	H	–	1.6	3.9	7.6	–	3.5	–	23.0	742	594
SE1-(1995)	S1	1250	–	–	–	437	3.4	–	–	1341	1247
SE1-(1996)	S2	1220	4.3	4.8	4.8	393	3.4	–	–	1236	1241
SE1-(1998)	S3	1080	3.4	2.8	5.7	–	3.4	–	–	–	–

effect on soil fluxes. In this chapter, however, we focus on the effects of precipitation, temperature, and NPP on the variability in annual soil CO_2 efflux among the EUROFLUX forests.

12.2.1 Effect of Precipitation

Globally, soil CO_2 efflux correlates significantly with annual precipitation (Raich and Schlesinger 1992). Among the EUROFLUX forests, however, this relation was not observed (Fig. 12.5). It should be understood that annual precipitation is a poor estimate of moisture availability. In the drought-stressed Mediterranean sites, e.g., precipitation is relatively large, but occurs in winter. Thus, moisture availability is quite high in winter, but extremely low in summer, which annual precipitation does not indicate. We believe that the actual evapotranspiration (ET) rate, or the ratio of actual/potential ET, provides better estimates of moisture availability, but these were not available.

12.2.2 Effect of Soil Temperature

Although temperature was positively correlated with soil CO_2 efflux in most of the sites, we found no positive trend among the different forests (Fig. 12.6). With the exception of the IT-2 site (Y in Fig. 12.6), total annual soil CO_2 efflux was even higher in the colder sites (Table 12.5). The enhanced fluxes in the colder sites may be explained by a combination a different factors. Firstly, in

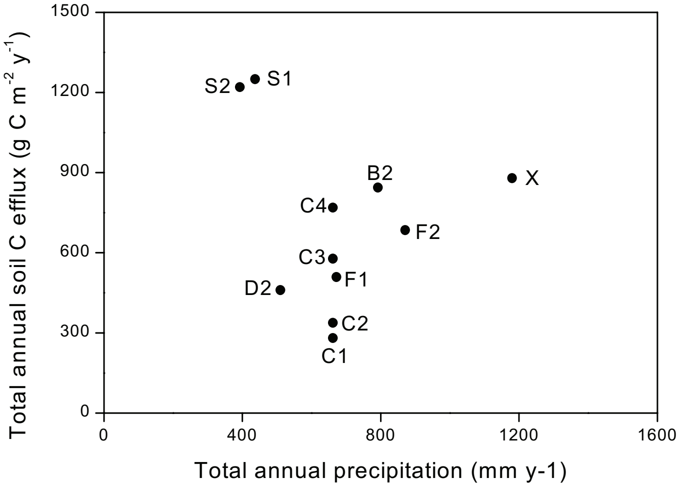

Fig. 12.5. Total annual soil CO_2 efflux versus total annual precipitation in the different EUROFLUX sites. Codes for different sites are explained in Table 12.5

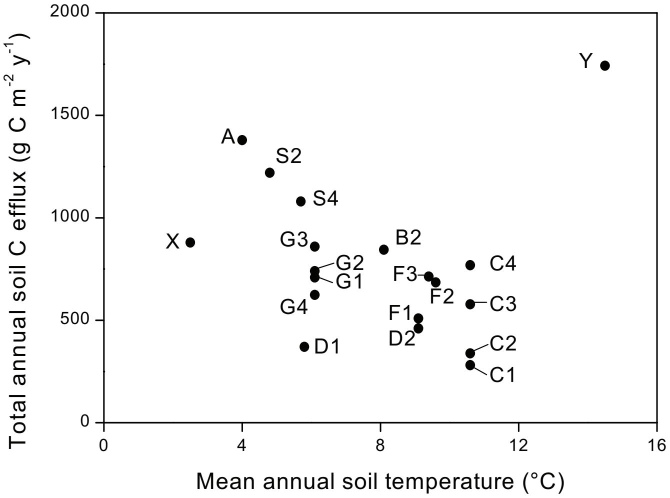

Fig. 12.6. Total annual soil CO_2 efflux versus mean annual soil temperature in the different EUROFLUX forests. Codes for different sites are explained in Table 12.5

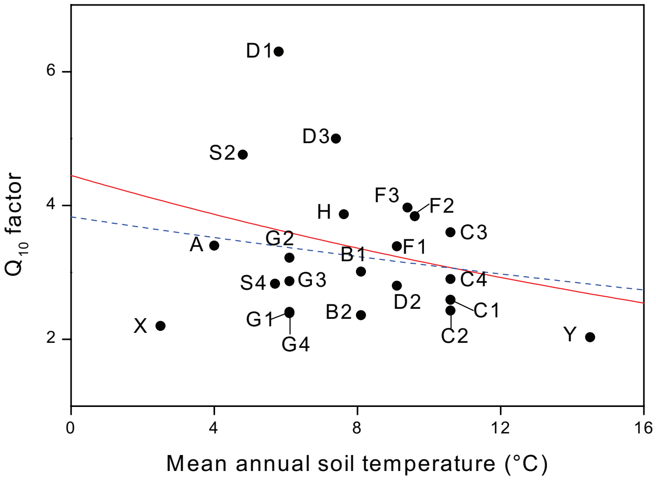

Fig. 12.7. Temperature sensitivity (Q_{10} factor) of soil CO_2 efflux versus mean annual soil temperature in the different EUROFLUX forests. Codes for different sites are explained in Table 12.5. The *plotted lines* represent negative exponential functions fitted to the entire data set (*dashed line*), and to the data set without the drought-stressed sites (*solid line*). See text for discussion of parameter values

agreement with previous studies (Schleser 1982; Kirschbaum 1995), we observed a (non-significant) negative trend in the temperature sensitivity of soil CO_2 efflux with increasing temperature (Fig. 12.7). Recent increases in global temperature will therefore have stimulated soil CO_2 efflux more at low than at high temperatures.

Secondly, soil CO_2 efflux is positively correlated with productivity (Raich and Schlesinger 1992), as is extensively discussed in Janssens et al. (2001b). Recent increases in temperature and atmospheric CO_2 concentrations have stimulated NPP directly, through enhanced photosynthetic rates, and indirectly, through the lengthening of the growing season (Myneni et al. 1997). Because temperature increases are larger in colder regions, productivity is stimulated more, and thus also soil CO_2 efflux is expected to be enhanced more.

Thirdly, soil drainage at the Swedish site (S2 and S4 in Fig. 12.6) has resulted in increased aeration that may have stimulated decomposition of native SOM.

Fourthly, enhanced decomposition rates in response to increasing temperature results in the release of more nutrients. This fertilizing effect will stimulate productivity (Schimel et al. 1996), but will probably have a stronger effect in the cold and nutrient-limited northern ecosystems than in the nitrogen-saturated ecosystems of western Europe.

Fifthly, the use of different methodologies is also likely to have contributed to this observation. Soil respiration at the two coolest sites was measured with the PP-Systems SRC-1 soil chamber, which may overestimate soil fluxes (Chap. 3; Le Dantec et al. 1999; Janssens et al. 2000).

Nevertheless, even among forests from temperate climates, we did not observe the expected positive relationship between annual soil CO_2 efflux and soil temperature (Fig. 12.6). The use of different techniques to measure soil CO_2 efflux (Chap. 3) is probably an important source of variability, but even among sites with identical measurement systems, no positive relationship with temperature was detected. Other factors that may have confounded the relation with temperature are differences in vegetation cover, site productivity, soil acidity and texture, quality and quantity of soil organic matter, and, of course, drought stress.

Both temperature sensitivity (Q_{10}) and basal rate (SR_{10}, efflux at 10 °C) of soil CO_2 efflux tended to decrease with mean annual soil temperature (Figs. 12.7, 12.8). A negative exponential function [$y=a \times \exp^{(b \times x)}$] was fitted to the data. The negative trend in Q_{10} with increasing soil temperature (dashed line in Fig. 12.7) was very weak and not statistically different from zero ($a=3.8$, $b=-0.021$, $R^2=0.041$, $P=0.364$, $n=22$). Exclusion of the two drought-stressed Mediterranean sites, where the Q_{10} factor was derived from a selected data set (without water stress), made the fitted relationship slightly more negative (solid line in Fig 12.7), but still not significantly different from zero ($a=4.45$, $b=-0.035$, $R^2=0.062$, $P=0.292$, $n=20$). A negative relationship between the Q_{10} values of soil respiration and soil temperature was also reported by Schleser (1982) and Kirschbaum (1995), and probably originates from the larger seasonal fluctuations of root and microbial biomass in colder climates. Wardle (1998) reviewed the literature on the temporal changes in microbial biomass and found that the most northern sites showed the highest

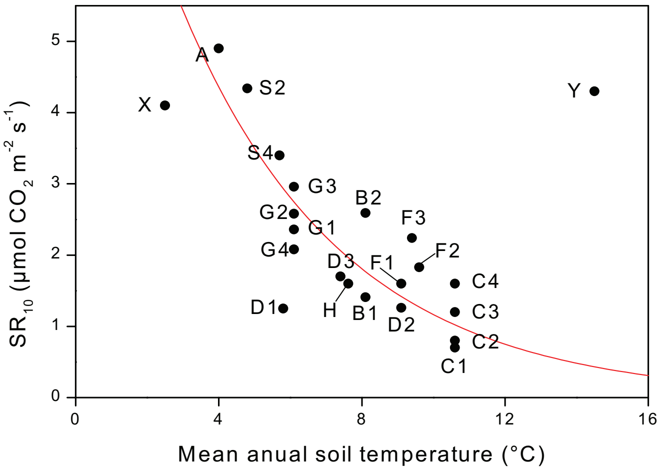

Fig. 12.8. Basal rate of soil CO_2 efflux (SR_{10}, flux rate at 10 °C) versus mean annual soil temperature in the different EUROFLUX forests. Codes for different sites are explained in Table 12.5. The *plotted line* represents the negative exponential function fitted to the data set without the drought-stressed sites. See text for discussion of parameter values

temporal variability. Ecosystems where the soil does not freeze over winter (with lower mortality due to frost) showed only small differences in microbial biomass during the year. The same probably holds for root biomass. Because the temporal changes in soil CO_2 efflux are highly dependent on root and microbial biomass, these observations may explain why soil CO_2 efflux is more sensitive to temperature in cooler climates.

The calculated Q_{10} values depend on the amplitude of the reference temperature (Kicklighter et al. 1994); thus, they are partly determined by the depth of the soil temperature measurements. Lower measurement depths have a smaller temperature range, and therefore a higher temperature sensitivity (Q_{10}). At shallower depths, soil temperature covers a broader range, which will result in a lower temperature sensitivity. Thus, small differences in the measurement depth may have introduced some variability in Fig. 12.7.

Except for the drought-stressed IT-2 site (Y), a decrease in base respiration rate with annual temperature was observed (Fig. 12.8). When excluding the two drought-stressed sites (X and Y), the exponential function fitted the data rather well and the decrease was significantly different from zero ($a=10.5$, $b=-0.22$, $R^2=0.691$, $P<0.001$, $n=20$). The decrease in base respiration rates in warmer sites is likely due to acclimation of roots and microorganisms to local climate. For the cooler climates, 10 °C is at the high end of the soil temperature range, whereas in the temperate region it is only slightly above the annual mean. This, combined with the higher temperature sensitivity of soil CO_2 efflux in the cooler climates, probably explains the sharp increase in base respiration rate at lower temperature.

12.2.3 Effect of Site Productivity

We assumed aboveground NPP (net primary productivity) to be a good representative of site productivity. In their review, Raich and Potter (1995) reported a significant positive correlation between soil CO_2 efflux and NPP on the global scale. This positive correlation between the total annual soil CO_2 efflux rates and NPP was also found among the EUROFLUX forests (P=0.09), as is shown in Fig. 12.9. This is not unexpected, since forests with high NPP are likely to have enhanced root activity and higher litter production, both resulting in high soil CO_2 efflux rates. For more information on the relation between soil respiration and productivity, the reader is referred to Janssens et al. (2001b).

However, increases in soil CO_2 efflux (e.g., due to temperature increases) may also stimulate NPP. Due to the enhanced decomposition, more nutrients will be released from the soil organic matter that become available for the trees. Because boreal forests are generally nutrient limited (Tamm 1985; Linder 1987), enhanced decomposition may thus fertilize these sites and stimulate NPP. The high NPP at the Swedish site might therefore be partly related to the high soil CO_2 efflux rates observed at that site (Table 12.5).

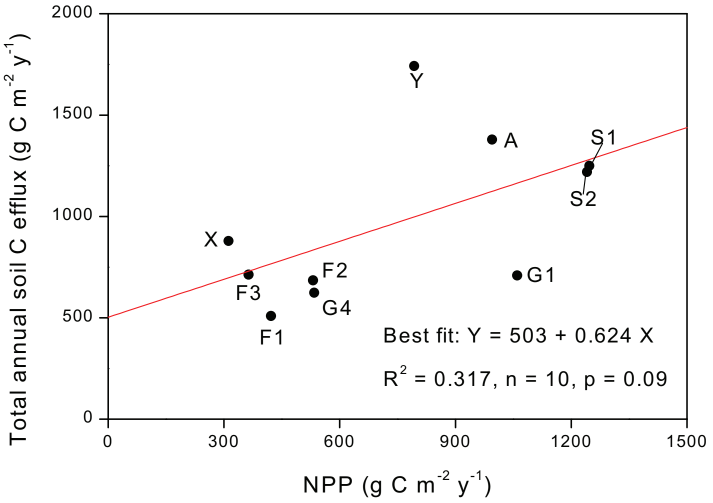

Fig. 12.9. Total annual soil CO_2 efflux rates versus aboveground NPP in the different EUROFLUX forests. Codes for different sites are explained in Table 12.5

12.3 Importance of Roots in Soil CO_2 Efflux

There is large uncertainty concerning the relative contribution of heterotrophic and root respiration to total soil CO_2 efflux. Reported estimates of the contribution of root respiration in forests average around 45 % (Landsberg and Gower 1997), but the estimates range from 22 % (Tate et al. 1993) to 90 % (Thierron and Laudelout 1996). Some of this variability is natural and may be related to differences in vegetation and/or soil type. Forests growing on soils with low organic carbon content will have a higher relative contribution of root respiration than primeval forests with a significantly larger soil carbon pool. Recently Boone et al. (1998) reported that the temperature sensitivity of root respiration is much higher than that of heterotrophic respiration. This was also found in the FR-1 site, where the Q_{10} value of root respiration was 3.86 and that of heterotrophic soil respiration was 2.34. These differences in temperature sensitivity are probably related to the larger temporal variability in root biomass compared to microbial biomass, and to the lower soil moisture content in summer, which would affect microbial respiration more than root respiration, because trees can extract water from deeper soil layers. Because of the different temperature sensitivities, the contribution of root respiration to total soil CO_2 efflux is likely to be higher in summer than in winter. This seasonal pattern was indeed observed at the FR-1 site (Fig. 12.10). Estimates of the relative contribution of root respiration obtained in different seasons are thus likely to be different, which could also add to the variability of the estimates found in literature.

Another, and probably larger source of variability in the estimates of the contribution of root respiration to the total soil CO_2 efflux, is the application

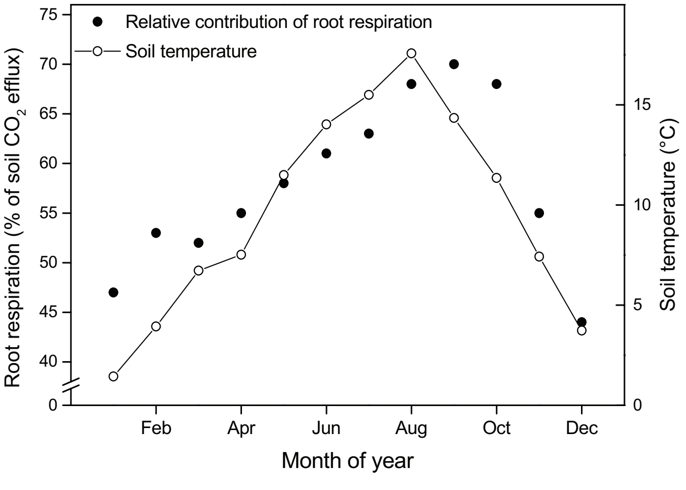

Fig. 12.10. Time series (1997) of soil temperature and of the relative contribution of root respiration to soil CO_2 efflux at the F-2 site

of different methodologies. Estimates of the contribution of root respiration have been obtained by scaling-up measurements of root respiration and comparing these with measured soil CO_2 efflux rates (Gansert 1994), by comparing soil CO_2 efflux in trenched and control plots (Ewel et al. 1987; Bowden et al. 1993; Boone et al. 1998; Epron et al. 1999b), by girdling trees and comparing soil CO_2 efflux below them with control plots (Högberg et al. 2001), by subtracting heterotrophic respiration estimated via laboratory incubations from the in situ measurements of soil CO_2 efflux (Edwards and Sollins 1973; Ewel et al. 1987; Thierron and Laudelout 1996), by extrapolating the regression of soil CO_2 efflux versus root biomass to zero root biomass (Kucera and Kirkham 1971; Behera et al. 1990), and from the ^{13}C and/or ^{14}C fingerprint of the respired CO_2 (Swinnen et al. 1994; Högberg and Ekblad 1996; Lin et al. 1999). The last method estimates rhizosphere respiration without disturbing the soil or the roots, and might therefore produce the best reckoning of the source of CO_2.

At the FR-1 beech site the contribution of root respiration to soil carbon efflux was estimated by comparing soil CO_2 efflux from small (2 × 1.5 m) trenched plots to efflux from undisturbed control areas. The treeless trenched plots were established by digging a trench (1 m depth) around each, lining the trench with a polyethylene film and filling it back. Soil CO_2 efflux was measured every 2 to 4 weeks in 1997 (Epron et al. 1999b). An empirical model ($y=a\,\theta_v\,e^{bT}$), fitted to the soil CO_2 efflux data was used to calculate annual soil CO_2 efflux from soil temperature (T) and soil water content (θ_v). The annual soil carbon efflux were 680 g C m^{-2} $year^{-1}$ in the main plot and 510 g C m^{-2} $year^{-1}$ in the trenched plots. Since trenching strongly influenced soil water content by eliminating tree transpiration, the annual soil carbon efflux on the trenched plots was corrected for differences in soil water content between trenched and control plots. In addition, respiration in the trenched plots was corrected for the decomposition of roots that were killed following trenching (Epron et al. 1999b). Thus root respiration was estimated to account for 60 % of soil C release (410 g C m^{-2} $year^{-1}$), representing 40 % of total ecosystem respiration and 30 % of gross primary productivity at this site.

At the BE-2 Scots pine site, the contribution of root respiration in summer was estimated indirectly by extrapolating the relation between soil CO_2 efflux and root biomass underneath the soil collar ($n=21$) to the Y-intercept (no roots). Thus, root respiration was estimated to account for 53 % of total soil CO_2 efflux when undergrowth was present and for 75 % when undergrowth was absent (Janssens and Ceulemans, unpubl.). The difference between the two cases was not related to differences in root respiration but to the enhanced heterotrophic respiration when undergrowth was present.

12.4 Conclusions

1. Soil temperature explained most of the temporal variability in soil CO_2 efflux in the majority of the EUROFLUX forests, but not in the drought-stressed sites. Empirical models explained 70–90 % of the seasonal variability in forests with limited drought stress, while they only explained 60–70 % in the drought-stressed Mediterranean sites.
2. Estimates of total annual soil CO_2 efflux by empirical modeling are not sensitive to the type of temperature or moisture regression. However, within a single year, large differences are found between the different regression functions.
3. We found no positive relationship between total annual soil CO_2 efflux and total precipitation or mean annual soil temperature among the different EUROFLUX forests.
4. Annual soil CO_2 efflux was positively correlated with NPP, suggesting that site productivity was more important than local climate in determining the differences in soil CO_2 efflux observed among the EUROFLUX forests. A positive trend was also observed with soil pH, while higher litter layer C/N ratios tended to have a negative effect on soil CO_2 efflux.
5. The relative contribution of root respiration to total soil CO_2 efflux was found to be higher in summer than in winter in the FR-1 site, which was probably related to the higher temperature sensitivity of roots.

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