

**Spatial and seasonal
variability of soil
respiration**

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Spatial and seasonal variability of heterotrophic and autotrophic soil respiration in a winter wheat stand

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Abstract

Soil respiration (R_s), the sum of respiration by soil organisms (R_h) and roots (R_a), is known to be highly variable in both, space and time. There is less information available about the behaviour of R_h and R_a in time and particularly in space. The objective of this study was to quantify the contribution of each component to the temporal and spatial variability of soil respiration in a winter wheat stand. We measured soil respiration from March to July 2009 by closed-dynamic chambers for 61 sampling points in a 50×50 m plot in a winter wheat stand close to Jülich, Germany. Each sampling point was equipped with a 7 cm soil collar to measure total R_s and a 50 cm soil collar to exclude roots and to measure R_h only. R_a was assumed to equal $R_s - R_h$. Simultaneously, soil temperature and soil water content were measured in 6 cm depth. Biweekly the temporal development of the leaf area index was measured. On average, the heterotrophic contribution to R_s was 69% and thus higher than the autotrophic contribution. Seasonal changes of soil temperature and especially water content explained well the temporal variability of R_s ($r^2=0.74$) and R_a ($r^2=0.80$). Spatial variability of R_a was on average much higher (CV=88%) than the spatial variability of R_h (CV=30%). However, R_h was mainly randomly distributed in space, whereas R_a showed spatial autocorrelation. Spatial correlation and cross-variograms showed a significant spatial dependence of R_s on R_a . From our results we concluded that spatial variability of soil respiration in a winter wheat stand represented mainly the spatial variability of the autotrophic component.

1 Introduction

The global atmospheric carbon concentration increased from a preindustrial value of 280 ppm to 379 ppm in 2005, mainly caused by the consumption of fossil fuels (IPCC, 2007). Soils, containing twice as much carbon as the atmosphere, could strongly change the carbon dioxide concentration in the atmosphere due to altered carbon losses (Smith et al., 2008).

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The emission of carbon dioxide from soils, usually referred to as soil respiration (R_s), is the second largest flux of carbon between terrestrial ecosystems and the atmosphere, constituting 20–38% of the annual atmospheric input of $\text{CO}_2\text{-C}$ (Raich and Schlesinger, 1992). The sources of soil respiration are mainly of heterotrophic (R_h) and autotrophic (R_a) nature:

$$R_s = R_h + R_a \quad (1)$$

Microbial decomposition of soil organic matter represents the heterotrophic part, whereas the autotrophic part is the result of the metabolism of plant roots (Tang and Baldocchi, 2005). Here, we include the respiration of root exudates, e.g. by mycorrhizal fungi, to R_a despite the heterotrophic nature of these organisms (Andersen et al., 2005). This definition allows for a robust measurement methodology and is relevant for an adequate analysis of plant effects on spatial variability. The separation of R_s into its heterotrophic and autotrophic components remains an essential research challenge for the understanding and the modelling of the global carbon cycle and to estimate its response to climate change (Baggs, 2006). Different partitioning methods exist to separate R_s into R_h and R_a (Hanson et al., 2000). According to Kuzyakov (2006) they can be subdivided into two main groups: 1) non-isotopic methods, e.g. root-exclusion (e.g. Moyano et al., 2007) or model-based analysis of eddy-covariance measurements (e.g. Aubinet et al., 2009), and 2) isotopic methods, e.g. pulse labelling (e.g. Saproinov and Kuzyakov, 2007) or bomb-derived ^{14}C (e.g. Gaudinski et al., 2000).

The proportions of R_h and R_a vary between ecosystems and crop types. For example Wang and Fang (2009) analysed 36 grassland data-sets and reported that on average 36% of R_s originates from autotrophic sources. For forest sites, the fraction of R_a varies between 5–90% (Bond-Lamberty et al., 2004). At global scale, the autotrophic contribution to R_s varies between 10–90% (Hanson et al., 2000).

The seasonal variability of R_s is mainly driven by soil temperature (e.g. Lloyd and Taylor, 1994; Davidson et al., 1998; Fang and Moncrieff, 2001; Davidson and Janssens, 2006) and to a lesser extent by soil water content (e.g. Davidson et al., 1998, 2000;

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Tang et al., 2006; Almagro et al., 2009). The relation between soil temperature and soil respiration is often described by an exponential function (e.g. Lloyd and Taylor, 1994; Davidson et al., 1998). However, high temperatures in the summer can inhibit microbial activity and thus reduce soil respiration due to the mortal effect of soil temperatures higher than 38 °C (Fang and Moncrieff, 2001). An influence of soil water content on R_s is mainly observed during periods with extreme soil water contents (Reichstein et al., 2002; Borken et al., 2003). During droughts, microbial activity is inhibited due to the reduced water availability resulting in lower rates of R_h . During wet periods the soil is almost saturated, which results on one hand in low concentrations of oxygen in the soil inhibiting microbial activity and thus R_h . On the other hand the transport of gases in the soil, e.g. carbon dioxide, is reduced inhibiting both R_h and R_a . The relationship between soil water content and R_s can be described with a quadratic function (Qi and Xu, 2001; Sotta et al., 2004; Chang et al., 2008; Zimmermann et al., 2009).

Soil temperature and soil water content often control R_s not as independent but as interacting variables. Droughts occur mainly in the summer season whereas soil water content is typically higher in the autumn and winter season. Apart from soil temperature and soil water content as abiotic factors, the temporal variability of the autotrophic component of R_s is mainly related to biotic factors, e.g. gross primary production (GPP), leaf area index and root biomass (Buchmann, 2000; Han et al., 2007; Bahn et al., 2008; Aubinet et al., 2009).

The spatial pattern of R_s is a mixture of the patterns of the heterotrophic and autotrophic component. R_a can increase the spatial variability of R_s , if the root system adds heterogeneity, depending on the land use type. For example crops planted in rows, e.g. maize, reveal higher rates of R_s close to the rows due to the increased root respiration (Rochette et al., 1991), adding a linear structure to the underlying structure of R_h . A quite similar case is the soil respiration in forests, where the respiration is higher close to the stems, due to increasing root density (Tang and Baldocchi, 2005) and higher amounts of litter (Fang et al., 1998). However, there is no information in literature about the proportion of heterotrophic and autotrophic spatial variability on the

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spatial variability of total R_S .

The objectives of the study were (1) to analyse the contribution of heterotrophic and autotrophic respiration to the seasonal variability of R_S , (2) to determine which of the two components, heterotrophic and autotrophic, mainly accounts for the spatial variability of R_S , and (3) to detect differences in the spatial correlation structure between the heterotrophic and the autotrophic component.

2 Methods

2.1 Experimental site and climate conditions

The experimental site (Fig. 1) was located in the agricultural area called "Jülicher Börde" near Selhausen, approximately 7 km SE of Research Centre Jülich, Germany (50° 52' 11" N, 6° 26' 57" E, 103 m a.s.l.). The site is characterised by a temperate climate with an average annual temperature of 9.9°C and an average annual precipitation of 698 mm. Sampling was done at a 50×50 m plot within an agricultural field cultivated with winter wheat which was harvested on 27 July 2009. The soil type was a Haplic Luvisol according to the World Reference Base for Soil Resources (FAO, 2006). A detailed description of the soil is given by Weihermüller et al. (2007).

2.2 Measurements

Weekly measurements of soil respiration, soil temperature and soil water content were carried out between 19 March and 27 July 2009 within the 50×50 m plot for 61 sampling locations, subdivided in 36 sample points located on a regular 10 m grid and 25 sample points randomly located in the 10×10 m subplots (Fig. 1). Soil respiration was measured using an automatic closed dynamic chamber system (LI 8100-103, LI-COR Biosciences, Lincoln, Nebraska, USA). An adaption period of 1 min to achieve an ambient CO₂ concentration inside the chamber-system was followed by a measurement period of 2 min for each collar.

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Permanently installed thermocouples were used to measure soil temperature (T) at 6 cm depth within the soil collars. Permanently horizontally installed 3-rod TDR-probes with a rod-length of 20 cm were used to simultaneously measure soil water content (θ) in 6 cm depth inside the soil collars. Water content was calculated using Topp's equation (Topp et al., 1980).

Green and brown leaf area index (LAI_g , LAI_b) were measured bi-weekly at three locations in the wheat field with a portable leaf area meter (LI-3000A, LI-COR Biosciences, Lincoln, Nebraska, USA) and averaged.

2.3 Partitioning of heterotrophic and autotrophic respiration

In this study, the partitioning of R_h and R_a was done by root exclusion (Bowden et al., 1993; Hanson et al., 2000; Tang et al., 2005; Baggs, 2006; Subke et al., 2006; Moyano et al., 2007). Each sampling location consisted of one 7 cm and one 50 cm soil collar (PP-H, 20 cm diameter), close to each other, to measure R_s and R_h , respectively. More than 80% of root biomass are located in the upper 50 cm of the soil (Wilhelm et al., 1982; Kätterer et al., 1993). Accordingly, the 50 cm collar inhibited a rooting inside the collar and we assumed that the corresponding CO_2 efflux represented R_h . The 7 cm collars allowed a rooting inside the collar and we assumed that the corresponding CO_2 efflux represents total R_s . According to Eq. (1), R_a was calculated as the difference between R_s and R_h . In the following, variables measured at locations of heterotrophic soil respiration (50 cm soil collars) are indicated by subscript h and variables measured at locations of total soil respiration (7 cm soil collars) are indicated by subscript s.

2.4 Soil temperature, water content and phenology controls on soil respiration

The relationship between R_s and T was modelled by an exponential function (Lloyd and Taylor, 1994):

$$R_s = ae^{bT} \quad (2)$$

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with parameters a and b . A potential function was used to model the relation between R_s and θ (Qi and Xu, 2001):

$$R_s = a\theta^c \quad (3)$$

with parameters a and c . The dependence of R_s on LAI was described by a simple linear function (Reichstein et al., 2003; Shi et al., 2006):

$$R_s = a + dLAI \quad (4)$$

with parameters a and d . Equations (2) and (3) were then combined to model the relation between R_s , T and θ (Tang et al., 2006):

$$R_s = ae^{bT} \theta^c \quad (5)$$

with parameters a , b , c . Equation (5) combined with Eq. (4) was used to additionally include the LAI:

$$R_s = ae^{bT} \theta^c + dLAI \quad (6)$$

with the additional parameter d . The differential evolution algorithm (Storn and Price, 1997) was used for model fitting. For model selection we calculated the Akaike information criterion (AIC, Akaike, 1973, 1974):

$$AIC = -2\ln L_{\text{Max}} + 2k \quad (7)$$

where $\ln L_{\text{Max}}$ is the maximised log-likelihood function and k is the number of fitted parameters. In case of a least squares estimation with normally distributed errors, the AIC is calculated using the sum of squares error of the fitted model:

$$AIC = n \ln \left(\frac{\sum_{i=1}^n (y_{\text{obs},i} - y_{\text{est},i})^2}{n} \right) + 2(k+1) \quad (8)$$

where n is the sample size and y_{obs} and y_{est} are the observed and estimated values. The equation uses $k+1$ instead of k because the variance needs to be estimated. Due

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to the small sample size in the present study ($n/k < 40$) we used the corrected Akaike information criterion (AIC_c) proposed by Hurvich and Tsai (1989):

$$AIC_c = AIC + \frac{2(k+1)(k+2)}{n-k-2} \quad (9)$$

Finally, the most suitable model is the one with the minimum AIC_c value.

2.5 Spatial analysis of states and fluxes

Normal distribution of the data is a precondition for geostatistical analysis (Cressie and Hawkins, 1980) wherefore soil respiration data was log-transformed prior to spatial and temporal detrending and outlier detection. A temporal trend existed in the data due to the measurement duration of 3 h to sample the 61 locations. Respiration and temperature increased almost linearly over time since the measurements usually started at the morning and ended at noon. This temporal trend was removed by fitting a linear function to the data and detrending the data to the starting time. Due to the gentle slope in the plot (Fig. 1) a small linear spatial trend existed in the data which was removed by detrending the data to the same elevation. For detecting spatial outliers we used the basic *Median Algorithm* described by Chen et al. (2008) and extended it by a dynamic neighbour estimation and a spatial weighting of the neighbourhood function based on Kou et al. (2006). We chose a radius of 15 m for the dynamic neighbour estimation and $\alpha=0.05$ for the outlier criterion. At maximum 5 outliers per sampled dataset were detected and removed. The presence of outliers was mainly the result of erroneous measurements, e.g. due to incomplete contact between collar and chamber.

2.5.1 Variogram estimation

Geostatistical methods are common techniques to analyse spatial structure, behaviour and interactions of variables (Journel and Huijbregts, 1978; Goovaerts, 1998, 1999; Diggle and Ribeiro, 2007). Basic tool for the spatial analysis is the semivariogram

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describing the spatial autocorrelation of a variable. The classical variogram estimator based on Matheron (1963) defines the semivariance $\gamma(h)$ as the mean squared difference between a set of data pairs for each specific lag distance h :

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_i + h)]^2 \quad (10)$$

5 where $N(h)$ is the number of data pairs in the given lag, $z(x_i)$ is the measured value at location x_i and $z(x_i + h)$ is the measured value at location $x_i + h$. Due to the necessary log-normalisation of the soil respiration data a robust estimation of the semivariance following the approach of Cressie and Hawkins (1980) was applied:

$$\gamma(h) = \frac{\left\{ \frac{1}{|N(h)|} \cdot \sum_{i=1}^{N(h)} |Z(x_i) - Z(x_i + h)|^{1/2} \right\}^4}{2 \left(0.457 + \frac{0.494}{N(h)} \right)} \quad (11)$$

10 where the constants 0.457 and 0.494 are based on the normality assumption.

Plotting the associated semivariance $\gamma(h)$ for each specific lag h gives the sample variogram which could be fitted by models with three characteristic parameters: the nugget variance c_0 , the structural variance c_1 and the range a_1 . For estimating variogram parameters c_0 , c_1 and a_1 we fitted a spherical model to the sample variogram:

$$15 \quad \gamma(h) = \begin{cases} c_0 + c_1 \left[\frac{1.5h}{a_1} - 0.5 \left(\frac{h}{a_1} \right)^3 \right] & \text{for } h \leq a_1 \\ c_0 + c_1 & \text{for } h > a_1 \end{cases} \quad (12)$$

The nugget c_0 represents the sum of small-scale variability and measurement error. The structural variance c_1 represents spatial variability which exists inside range a_1 . Therefore, the range a_1 is also referred to as spatial autocorrelation length. For distances larger than the range spatial autocorrelation is not given and semivariance
20 equals the sum of nugget- and structural variance. For the interpretation of spatial

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variability it is necessary to consider the magnitude of spatial dependence by calculating the nugget coefficient n_c (Robertson and Freckman, 1995; Morris, 1999; Hirobe et al., 2001; Mori and Takeda, 2003):

$$n_c = \frac{c_0}{c_0 + c_1} \quad (13)$$

where the nugget variance c_0 is related to the total variance ($c_0 + c_1$). If n_c is smaller than 0.25 the variable shows strong spatial dependence, if it varies between 0.25 and 0.75 there is only moderate spatial dependence and if n_c is larger than 0.75 there is basically no spatial dependence (Cambardella et al., 1994).

The spatial correlation between two variables z_i and z_j and their variation in space is given by the cross-semivariance:

$$\gamma_{i,j}(h) = \frac{1}{2N(h)} \sum_{\alpha=1}^{N(h)} [z_i(x_\alpha) - z_i(x_\alpha + h)] [z_j(x_\alpha) - z_j(x_\alpha + h)] \quad (14)$$

Again, the differential evolution algorithm (Storn and Price, 1997) was used to fit the spherical model to the sample variogram. Robust variogram estimation and spherical model fitting were implemented in GNU Octave (Eaton, 2002). Cross-variograms were calculated using the *variogram*-function of the *gstat*-package (Pebesma, 2004) in the *R*-environment (R Development Core Team, 2005). To calculate an average range of spatial autocorrelation, we selected measurement dates for which the following two criteria applied: i) the coefficient of determination (r^2) between the sample variogram and the fitted spherical model function was higher than 0.5 to avoid the impact of erroneous variogram fittings on the average range estimate. ii) the nugget coefficient (n_c) was lower than 0.75 to ensure at least a moderate spatial dependence.

2.5.2 Spatial mapping of states and fluxes

Compared to kriging as an estimation approach, simulation approaches focus on the reproduction of the statistics and geostatistics of the observation, e.g. histogram and

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variogram (Goovaerts, 1999). Conditional sequential Gaussian simulation (SGS, Rossi et al., 1993; Goovaerts, 2000; King, 2000) was used for mapping the spatial pattern of soil respiration. A simulation is conditioned when it reproduces measured data at measured locations. The basic steps of SGS are well described by Deutsch and Journal (1998); King (2000); Goovaerts (2001). SGS was done using the *krige*-function of the *gstat*-package (Pebesma, 2004). The simulated fields included 2000 nodes and we generated 100 realizations for each simulated data set. From this, the realisation was chosen which best reproduced the statistics of the observation.

3 Results and discussion

3.1 Seasonal variation of total, heterotrophic and autotrophic soil respiration

During the measurement period between 19 March and 27 July 2009, R_s was on average $2.68 \pm 0.98 \mu\text{mol m}^{-2} \text{s}^{-1}$. The standard deviation represents the standard deviation of the field mean during the season. R_s showed a characteristic seasonal variation (Fig. 2a) and ranged between $1.06 \pm 0.49 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $5.04 \pm 3.03 \mu\text{mol m}^{-2} \text{s}^{-1}$. Between March and the middle of May R_s increased and showed the maximum on 15 May when also the LAI_g of winter wheat was highest (Fig. 2e). After plant senescence, R_s decreased and fluxes of about $2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ were measured. R_h was rather constant during the measurement period with an overall average of $2.07 \pm 0.38 \mu\text{mol m}^{-2} \text{s}^{-1}$. Compared to R_s , the seasonal variation of R_h was smaller and ranged between $1.32 \pm 0.34 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $2.81 \pm 1.03 \mu\text{mol m}^{-2} \text{s}^{-1}$. As expected, after plant senescence for the last three sampling dates in July R_h was equal to R_s . The seasonal variation of R_a was equal to the seasonal variation of R_s . Compared to R_h the average flux of R_a was smaller with $0.93 \pm 0.82 \mu\text{mol m}^{-2} \text{s}^{-1}$ and showed fluxes up to $2.59 \pm 1.48 \mu\text{mol m}^{-2} \text{s}^{-1}$ (22 April).

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Several studies on soil respiration in winter wheat focused on total R_s rather than on the single contributions of R_h and R_a . Beyer (1991) measured R_s in winter wheat from June to December 1986 at two sites in Schleswig-Holstein, Germany. He also observed a characteristic increase of R_s during the summer and a decrease during autumn and winter. However, their measured fluxes of R_s were smaller with a maximum of around $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ in August, which might be attributed to lower temperatures during summer and to a lower organic carbon content of the soil. R_s measured by Rochette et al. (1991) from May to August 1989 in a spring wheat field in Ottawa, Kanada, was higher with an average efflux of $6.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ and ranged between $2.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $11.9 \mu\text{mol m}^{-2} \text{s}^{-1}$. However, soil temperature was much higher during the season ranging between 20°C and 33°C from June to September. Comparable fluxes of R_s were measured by Moureaux et al. (2008) in a wheat plot in Belgium in 2005. Their measured fluxes ranged between 2 and $3 \mu\text{mol m}^{-2} \text{s}^{-1}$ from May to August 2005.

The strong decrease of R_s and R_a on 5 May may have two reasons. On one hand, this might be the result of reduced photosynthetic activity of the plants due to an overcast sky. On the other hand, also soil water content showed a clear decrease (Fig. 2d) which probably caused stress on root activities and inhibited root respiration as reported by Epron et al. (1999); Rey et al. (2002); Saiz et al. (2006).

The autotrophic contribution to total soil respiration (Fig. 2b) was highest in April with 60% and decreased to almost zero at plant senescence. During June the autotrophic contribution increased up to a second maximum of 40% and decreased afterwards down to zero at the middle of July when only heterotrophic respiration occurred. This needs to be seen against the background of the temporal spacing of the measurement dates because they allow to track the seasonal development of respiration, but of course not the short-time variations occurring between the measurement dates. Cumulated values of R_s , R_h and R_a between April and August were 342 g C m^{-2} , 236 g C m^{-2} and 106 g C m^{-2} , respectively, equivalent to relative contributions of 69% for R_h and 31% for R_a . The study by Moureaux et al. (2008) reported cumulative R_s , R_h and R_a from November 2004 to July 2005 of 520 g C m^{-2} , 230 g C m^{-2} and 290 g C m^{-2} ,

respectively. The resultant autotrophic contribution to R_s was 56%. Shi et al. (2006) modelled R_s and R_h in the growing season by two temperature functions valid for the growing and non-growing season, respectively. From the difference between modelled R_s and R_h they calculated R_a and found an autotrophic contribution of 45%. The lower average contributions of R_a we detected could be explained by the fact that at the beginning of the measurements significant contributions of R_a were already observed and no measurements of R_a were performed in the early growing period.

Significant differences in soil water content between the neighbouring soil collars were observed during the study (Fig. 2d). It was to be expected that these water content differences were caused by root water uptake in the 7 cm soil collars which lead to lower water contents in the 7 cm collars. Right at the beginning of the growing season, when the root system of the plants was in the starting phase of development, lower water contents in the 50 cm collars were detected. This could partly be explained by installation effects of the TDR-probes in the 50 cm collars, e.g. the rods of the probes were not fully in contact with the soil when installing them through the collar, leading to an underestimation of the water contents. At the end of May, the influence of root water uptake in the 7 cm collars was clearly detected, which caused lower water contents in the 7 cm soil collars.

3.2 Soil temperature, water content and phenology controls on soil respiration

The seasonal variation of soil respiration is mainly controlled by soil temperature changes (e.g. Lloyd and Taylor, 1994; Buchmann, 2000; Fang and Moncrieff, 2001; Reichstein et al., 2002; Subke et al., 2003; Reichstein et al., 2005; Davidson and Janssens, 2006; Savage et al., 2009) and are commonly described by an exponential function. A slightly negative relation between soil respiration and soil temperature was found in our study (Tables 1 and 2). This may be attributed to two reasons. First, the data set just represents 18 snapshots of the seasonal change of soil respiration. Second, other environmental drivers including moisture and plant development status as studied here, may act as confounding factors (Davidson et al., 1998). Analysing the

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residuals of the temperature model (Eq. 2) showed a positive linear relation between θ and R_s , R_h and R_a with $r^2=0.71$, $r^2=0.38$ and $r^2=0.71$, respectively. This water content influence is expressed by a significant positive correlation between soil respiration and water content (Table 1), which was highest for R_a with $r=0.80$ ($p<0.001$) in combination with a negative correlation between soil temperature and water content, which was significant for T_s and θ_s with $r=-0.69$ ($p<0.01$). Using soil water content to model the temporal behaviour of soil respiration (Eq. 3) resulted in a higher r^2 and a lower RMSE compared to the temperature model. Also the AIC_c decreased significantly and points to a more suitable model. Studies by e.g., Davidson et al. (1998); Borken et al. (2003); Savage and Davidson (2003); Martin and Bolstad (2005); Almagro et al. (2009); Herbst et al. (2009) also reported a strong influence of soil water content on soil respiration. Soil temperature and soil water content were negatively correlated because warm temperatures in summer are often accompanied by low soil water contents, whereas in winter, cold temperatures are accompanied by high soil water content values. Indeed, the full models considering all available explanatory variables yield temperature exponents of 0.005 and 0.026 for R_h and R_s , respectively. These would translate into Q_{10} values of 1.05 and 1.30. The unusual low value for R_h can clearly be attributed to the extremely high scatter of the relation between soil temperature and R_h , which forces the slope of a regression model to underestimate the underlying functional relation (Webster, 1997). The still quite low Q_{10} value for the full R_s model may in part be attributed to the same reason, but may also be taken as a support of a recent study suggesting lower temperature sensitivities of respiration than previously (Mahecha et al., 2010). Only R_a exhibits a negative temperature exponent even after considering soil water content and LAI. It is still debated whether root respiration is positively affected by temperature at all (Moyano et al., 2007).

Adding soil water content as an explanatory variable to the temperature model using Eq. (5) resulted in better estimates of R_s and R_a , however, not of R_h (Table 2, Fig. 3a–c). The relation of R_s and R_a with soil temperature and soil water content were significant ($p<0.001$) and explained 74% and 80%, respectively, of the seasonal variability of soil

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respiration. Similar coefficients of determination were reported by Tang et al. (2006) for explaining the seasonal variability of R_s by changes of soil temperature and soil water content in subtropical forests in Southern China. Similar to their findings our results indicate that accounting for both, temperature and water content, provided a more suitable model in terms of AIC_c compared to just accounting for either temperature or water content. Only 27% of the seasonal variability of R_h could be explained by temperature and water content which was similar to model R_h in dependence of water content only. Thus, modelling R_h with water content only was more suitable due to the smaller AIC_c .

Autotrophic respiration is likely also a function of the development status of the plant and its root system. As an easily accessible indicator of plant development status, LAI may be related to root respiration via a linear model (Reichstein et al., 2003, Eq. 4). In our case, R_s and R_a showed only a weak relation with LAI_g having coefficients of determination of 0.38 and 0.21, respectively (Table 2). This corroborates the findings of Hibbard et al. (2005) who analysed soil respiration from various Northern Hemisphere temperate ecosystems. They explained it by large variations in the autotrophic contributions to total R_s , which was also observed in our measurements (Fig. 2b). This was quite different to the findings of Reichstein et al. (2003) and Shi et al. (2006). They explained 83% and 69%, respectively, of the seasonal variations of R_s by temporal changes in LAI_g . This discrepancy might simply be explained by the extended observation period and the higher temporal resolution of the respiration measurements compared to our data.

Due to the rather weak relation between R_s and R_a with LAI_g and compared to the modelling without LAI_g the additional parameter explained only slightly more of the seasonal variability in R_s and R_a ($r^2=0.77$ and $r^2=0.81$, respectively). The increase of 17% and 19% for R_s and R_a , respectively, in terms of the AIC_c was higher than the decrease in the RMSE with 7% and 1% for R_s and R_a , respectively. Including the LAI_g to estimate R_s and R_a did not provide a more suitable model.

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3.3 Seasonal development of spatial variations

The standard deviation shows the similarity in the seasonal trend of the spatial variations of R_s and R_a (Fig. 4a). The autotrophic contribution to the spatial variations of R_s (Fig. 4b) was highest at the beginning of the growing season with relative contributions up to 90%. Afterwards the autotrophic contribution decreased linearly ($r^2=0.67$) and at the beginning of June the autotrophic and the heterotrophic contribution to the spatial variation of R_s were similar. In the following period the heterotrophic contribution dominated and increased until harvest. Considerably higher spatial variations of R_a mainly caused the spatial variations in total R_s (Fig. 4a, b).

The temporal trend of the spatial variations in terms of the coefficient of variation (CV) was also quite similar for R_s , R_h and R_a (Fig. 4c), except for the peak in R_a on 6 June (CV=502%) caused by a short drought period existing from the middle of May up to the beginning of June with subsequent rewetting just before the measurement (Fig. 2d). A second peak of spatial variation was observed on 15 July for the autotrophic component because the wheat was nearly ripened and at various locations R_a was close to zero. The coefficient of variation relates the standard deviation to the average. The very low average fluxes of R_a observed at 6 June and 15 July combined with rather mid-range standard deviations (Fig. 4a) therefore resulted in two extreme coefficients of variation. During the observation period such average fluxes close to zero were not detected for R_h . During the growing season the CV was on average much higher for R_a (CV=118%) than for R_h (CV=30%). Excluding the two extremes reveals a lower CV of 88% for R_a . Spatial variations of R_a decreased very slightly during April and increased until the middle of May caused by plant growth. Stoyan et al. (2000) reported high spatial variations in root weights of wheat at a 2 m² plot which were higher in June (CV=250%) than in April (CV=100%). They also found a significant correlation between root weight and R_s which was on average 0.63. A general pattern might exist for cropped systems with lower spatial variations of R_s at the beginning of plant growth when the root-system is not fully developed and higher variations at full-grown stage since it was also detected for maize (Han et al., 2007).

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A similar temporal behaviour was observed for total R_s even though less pronounced (Fig. 4c), because of the rather time-stable heterotrophic contribution. The average CV for R_s was 38%. Rochette et al. (1991) measured a similar spatial variability of R_s on a 26 ha wheat field in Canada with an average CV of 45%. In contrast, they found a clear decrease of the spatial variations during the growing season from the beginning of May to the middle of August caused by an uneven application of solid manure in May. Solid manure was not applied in our study. Less spatial variation of R_h compared to R_a may result from a more heterogeneous root distribution compared to a more homogeneous distribution of microbes and carbon. Katsalirou et al. (2010) found relatively low spatial variations of microbial biomass (CV=28%) at a 2-m transect (0.2 m intervals) in a wheat field in the Southern Great Plains, USA.

3.4 Spatial structure of soil respiration

The variogram analysis revealed differences in the spatial structures of R_h and R_a (Table 3). For R_h the nugget coefficient was larger than 0.75 for 12 out of 18 dates, pointing to a poor spatial autocorrelation in R_h . At 9 measurement dates the variogram showed a pure nugget effect indicating a random distribution of R_h in space. A minimum nugget coefficient of 0.03 for R_h was detected on 22 July. The predominantly random spatial structure of R_h was also detected by Rochette et al. (1991) and Herbst et al. (2009) for bare soil plots. Herbst et al. (2009) found an average n_c of 0.71 for 15 sampling dates between April and July 2007 at a 14×14 m bare plot. Rochette et al. (1991) detected a predominantly random structure of R_h at two bare fields of 25 and 40 ha. The reason for the predominantly random structure of R_h might be the small-scale spatial variability of the microbial communities and carbon pools (Nunan et al., 2002). However, it should also be seen against the background of the lower coefficient of variation compared to R_a and thus a larger influence of a potential error variance.

In contrast to R_h , we detected a moderate to strong spatial dependence of R_a . The n_c of R_a was smaller than 0.75 at 14 of the 18 measurement dates, 7 dates showed an $n_c < 0.25$. R_s showed predominantly moderate or no spatial dependence with $n_c > 0.25$

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(18 of 20 dates). At two dates (5 May and 15 July) a strong spatial dependence with $n_c < 0.25$ was detected.

Cambardella et al. (1994) and Goovaerts (1998) pointed out that spatial autocorrelation is linked with a strong scale dependence. Western and Blöschl (1999) showed that the apparent correlation length increases with increasing spacing between sample points, extent of the observation area and sampling volume referred to as “support”. The apparent variance increases with increasing extent, decreases with increasing support and is constant for different spacings. We operated with a support of 0.031 m^2 , an average spacing of 4.61 m and an extent of $50 \times 50 \text{ m}$. In case spatial dependence was detected, defined by $n_c < 0.75$ and $r^2 \geq 0.5$ of variogram model fit, the average range of spatial autocorrelation (a_1) of R_h was 11 m at the observed scale. Herbst et al. (2009) reported an average range of spatial autocorrelation of 2.7 m for R_h for an extent of $14 \times 14 \text{ m}$. Rochette et al. (1991) detected for R_h a correlation length of 20 m for one of their 1-m spacing transects. For R_a and R_s we observed an almost similar average range of spatial autocorrelation of 16.8 m and 18.0 m, respectively, being larger than the average range of R_h with 11 m. Stoyan et al. (2000) measured R_s in winter wheat and reported a range of spatial autocorrelation of 29 cm for a clearly smaller support of $1.76 \times 10^{-4} \text{ m}^2$ and an extent of 2 m^2 . Due to the smaller support of their sampling the detected spatial variation of R_s was higher compared to our findings. The authors attributed this to “hot- and cold-spots” of very high and low soil respiration rates that often lied within the sampling volume (Morris, 1999).

The simulated maps of R_s , R_h and R_a shown for the measurements on 5 May and 28 May (Fig. 5a–h) represent typical spatial patterns. The variograms (Fig. 5a,e) revealed highest spatial variations for the autotrophic component. R_a showed strong spatial dependence ($n_c = 0$), whereas R_h is totally random distributed in space showing a pure nugget. This caused a strong (5 May) and moderate (28 May) spatial dependence of R_s as a mixture of the autotrophic and heterotrophic pattern. The ranges of spatial autocorrelation for R_a and R_s were 13.7 m and 7.4 m, respectively, on 5 May. On 28 May ranges were 7.5 m and 10.5 m, respectively, being shorter than the respective

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average range of spatial autocorrelation detected in our data. In contrast to spatial structures in the maps of R_a and R_s , the map of R_h represents random noise. The third mapping of R_s , R_h and R_a shown for the measurements on 20 May (Fig. 5j–l) represents a rather exceptioned state of spatial autocorrelation. Variograms showed that the nugget of R_s with 0.26, R_h with 0.34 and R_a with 0.10 were quite similar indicating moderate spatial dependence also for R_h . There were differences in the range of spatial autocorrelation with the highest range of 24 m detected for R_a , followed by R_s with 19 m and R_h with 9 m. Consequently, the spatial pattern of R_h again reveals a more random characteristic than the patterns of R_s and R_a . Due to the spatially homogeneous planting of winter wheat characteristic row-interrow patterns detected by Rochette et al. (1991) as a result of higher fluxes close to the rows, were not observed. Nevertheless, the autotrophic component showed high spatial variations and a clear spatial dependence which might be attributed to e.g. heterogeneity in the root system. To detect the source of the spatial structure of R_a in winter wheat spatial information about e.g. LAI and root density is needed.

As shown before, the spatial variation of R_s was mainly influenced by the autotrophic spatial variations. The spatial distribution of R_s was highly correlated with the spatial distribution of R_a (Fig. 6a). At the beginning of the growing season the coefficient of correlation in space was highest between R_s and R_a with $r=0.80$ and was almost constant until the middle of May. Afterwards the spatial correlation fluctuantly decreased to values of about 0.55 due to the decrease of autotrophic contributions to R_s as a result of plant senescence. Generally, the spatial pattern in R_s was stronger correlated to R_a than to R_h . The spatial correlation between R_s and R_h was lowest at the beginning of the growing season ranging between 0 and 0.20 and increased towards the end of the growing season when values ranged between 0.20 and 0.40.

Cross-variograms were calculated to analyse the spatial cross-correlation of R_s with R_h and R_a , respectively. The cross-variograms predominantly revealed a clear spatial dependence of R_s from R_a whereas the cross-variograms between R_s and R_h showed predominantly pure nuggets and thus no spatial cross-correlation. As an example,

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cross-variograms between R_s and R_a and R_h , respectively, on 5 May are shown in Fig. 6b. R_s showed a strong spatial dependence on R_a up to a range of 12.3 m, while no spatial dependence of R_s on R_h was observed.

Due to the setup-based distance between the soil collars of R_s and R_a and the detected stochastic spatial variability of R_h , it was to be expected that the indirect determination of R_a (Eq. 1) adds small-scale variability to the spatial pattern of R_a . Thus, the variograms for R_a represent a conservative estimate of its actual spatial dependence. The fact that computed R_a values exhibited stronger spatial dependence than both, R_s and R_h , underlines the dominating role of plant roots in determining soil respiration patterns and is reflected in the high spatial dependence of the spatial pattern of R_s from R_a .

4 Conclusions

From the observations of the spatially averaged fluxes in time we conclude that the seasonal changes of total R_s in winter wheat result from a temporally more variable autotrophic component compared to a rather time-stable heterotrophic component. Soil temperature and water content seasonal changes explained 74% and 80% of the temporal variability in total and autotrophic soil respiration, respectively.

We detected high spatial variations in the autotrophic component, attributed to the heterogeneity in local root development, which then mainly caused the variability of total soil respiration in space. During the final period of plant growth, when the root system is almost fully developed, autotrophic spatial variations are at maximum.

Total soil respiration and the autotrophic component showed moderate to strong spatial dependence in contrast to a predominantly random distribution of R_h in space. From high correlation between the spatial patterns of total soil respiration and the autotrophic component we conclude, that the pattern of total soil respiration basically resembles the autotrophic pattern. The lack of spatial autocorrelation in the heterotrophic component pattern is mostly responsible for the stochastic variations in the total soil respiration pattern.

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In conclusion, the observations prove that the spatial and seasonal variability of soil respiration in winter wheat basically originates from the variability of the autotrophic component.

All this indicates that chamber-based measurements of total soil respiration in cropped systems require an adequate spatial sampling design accounting for the spatial autocorrelation resulting from the autotrophic component. Further, for those periods when spatial variability of autotrophic and consequently total soil respiration is at maximum, sampling at a high spatial density is required in order to ensure representative average fluxes. However, concerning the spatial variability this may in part be a specific result for winter wheat. Other crops planted in rows would add another component to the spatial variation of fluxes.

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Table 1. Correlation matrix of soil respiration, soil temperature, water content and leaf area index.

	R_s	R_h	R_a	T_h	T_s	θ_h	θ_s	LAI _g	LAI _b
R_s		0.45	0.91***	-0.61*	-0.10	0.41	0.51*	0.62**	0.38
R_h	0.45		0.04	-0.02	0.10	0.53*	0.32	0.38	-0.04
R_a	0.91***	0.04		-0.70**	-0.72***	0.22	0.8***	0.46	-0.79***
T_h	-0.61*	-0.02	-0.70**		1.00***	-0.25	-0.55	-0.89***	0.77***
T_s	-0.10	0.10	-0.72***	1.00***		-0.17	-0.69**	-0.37	0.82***
θ_h	0.41	0.53*	0.22	-0.25	-0.17		0.52*	0.38	-0.02
θ_s	0.51*	0.32	0.80***	-0.55	-0.69**	0.52*		0.29	-0.83***
LAI _g	0.62**	0.38	0.46	-0.89***	-0.37	0.38	0.29		-0.31
LAI _b	-0.38	-0.04	-0.79***	0.77***	0.82***	-0.02	-0.83***	-0.31	

R_s : total soil respiration, R_h : heterotrophic soil respiration, R_a : autotrophic soil respiration, T_h : soil temperature in 6 cm depth at locations of heterotrophic soil respiration, T_s : soil temperature in 6 cm depth at locations of total soil respiration, θ_h : water content at 6 cm depth at locations of heterotrophic soil respiration, θ_s : water content at 6 cm depth at locations of total soil respiration, LAI_g: green leaf area index, LAI_b: brown leaf area index, RMSE: root mean square error, r : coefficient of correlation, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

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Table 2. Regression parameters and statistics for the seasonal relationship between soil respiration, soil temperature, water content and leaf area index.

Variables	Eq.	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	RMSE	<i>r</i> ²	AIC _c	<i>p</i>
$R_h=f(T_h)$	(2)	2.11	0	–	–	1.34	0.00	–26.9	
$R_h=f(\theta_h)$	(3)	8.01	–	0.957	–	1.32	0.27	–34.3	*
$R_h=f(T_h, \theta_h)$	(5)	7.56	0.005	0.968	–	1.15	0.27	–28.4	**
$R_a=f(T_s)$	(2)	1.77	–0.048	–	–	3.04	0.55	–2.5	***
$R_a=f(\theta_s)$	(3)	84.33	–	3.159	–	1.82	0.68	–20.0	***
$R_a=f(LAI_g)$	(4)	0.37	–	–	0.173	3.00	0.21	–4.8	
$R_a=f(T_s, \theta_s)$	(5)	164.74	–0.007	2.915	–	1.43	0.80	–21.2	***
$R_a=f(T_s, \theta_s, LAI_g)$	(6)	128.19	–0.009	2.478	–0.003	1.42	0.81	–17.1	***
$R_s=f(T_s)$	(2)	3.14	–0.008	–	–	4.17	0.01	5.9	
$R_s=f(\theta_s)$	(3)	15.98	–	1.138	–	1.94	0.72	–17.8	***
$R_s=f(LAI_g)$	(4)	2.02	–	–	0.282	3.37	0.38	–3.8	**
$R_s=f(T_s, \theta_s)$	(5)	18.02	–0.012	1.102	–	1.85	0.74	–13.1	***
$R_s=f(T_s, \theta_s, LAI_g)$	(6)	15.35	0.026	1.470	0.140	1.72	0.77	–10.9	***

R_s : total soil respiration, R_h : heterotrophic soil respiration, R_a : autotrophic soil respiration, T_h : soil temperature in 6 cm depth at locations of heterotrophic respiration, T_s : soil temperature in 6 cm depth at locations of total soil respiration, θ_h : water content at 6 cm depth at locations of heterotrophic respiration, θ_s : water content at 6 cm depth at locations of total soil respiration, LAI_g: green leaf area index, Eq.: model equation, *a–d*: fitted parameters, RMSE: root mean square error, *r*²: coefficient of determination, AIC_c: corrected Akaike Information Criterion, *p*: p-value: * *p*<0.05, ** *p*<0.01, *** *p*<0.001.

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Table 3. Variogram parameters of soil respiration for selected sampling dates.

date	Total soil respiration (R_s)					Heterotrophic soil respiration (R_h)					Autotrophic soil respiration (R_a)				
	c_0	c_1	n_c	a_1	r^2	c_0	c_1	n_c	a_1	r^2	c_0	c_1	n_c	a_1	r^2
16 Apr	0.009	0.012	0.43	7.6	0.09	0.010	0.000	1.00	0.0	0.00	0.025	0.018	0.59	14.4	0.55
22 Apr	0.021	0.003	0.87	17.9	0.03	0.019	0.004	0.82	35.1	0.45	0.082	0.011	0.88	23.6	0.57
30 Apr	0.004	0.013	0.26	13.1	0.74	0.016	0.000	0.99	22.7	0.20	0.033	0.012	0.73	19.1	0.21
5 May	0.002	0.030	0.06	7.4	0.63	0.016	0.000	1.00	0.0	0.00	0.000	0.225	0.00	13.7	0.77
13 May	0.045	0.034	0.57	26.0	0.46	0.016	0.012	0.57	10.0	0.21	0.021	0.106	0.16	23.6	0.73
20 May	0.009	0.027	0.26	19.0	0.93	0.007	0.014	0.34	8.7	0.81	0.006	0.052	0.10	24.1	0.96
27 May	0.020	0.000	1.00	0.0	0.00	0.010	0.003	0.76	23.3	0.64	0.005	0.134	0.04	11.7	0.83
28 May	0.006	0.011	0.35	10.5	0.72	0.019	0.000	1.00	0.0	0.00	0.000	0.094	0.00	7.5	0.71
3 Jun	0.015	0.002	0.86	23.2	0.12	0.002	0.009	0.21	10.9	0.90	0.008	0.011	0.42	19.5	0.88
17 Jun	0.003	0.006	0.36	23.1	0.95	0.016	0.000	1.00	0.0	0.00	0.082	0.054	0.60	8.7	0.51
24 Jun	0.022	0.000	1.00	0.0	0.00	0.004	0.020	0.18	6.1	0.10	0.000	0.078	0.00	11.2	0.30
1 Jul	0.005	0.003	0.63	14.6	0.14	0.015	0.000	1.00	0.0	0.00	0.003	0.109	0.03	4.7	0.00
15 Jul	0.005	0.015	0.23	35.1	0.78	0.026	0.000	1.00	0.0	0.00	0.007	0.004	0.62	28.1	0.56
22 Jul	0.019	0.000	1.00	0.0	0.00	0.000	0.015	0.03	13.4	0.84	0.004	0.006	0.44	11.8	0.84

c_0 : nugget, c_1 : structural variance, n_c : nugget coefficient ($c_0 (c_0+c_1)^{-1}$), a_1 : range of spatial autocorrelation, r^2 : coefficient of determination of fit. Values for c_0 and c_1 are given in $\log_{10} (\mu\text{mol m}^{-2} \text{s}^{-1})^2$ and values given for a_1 are given in meters.

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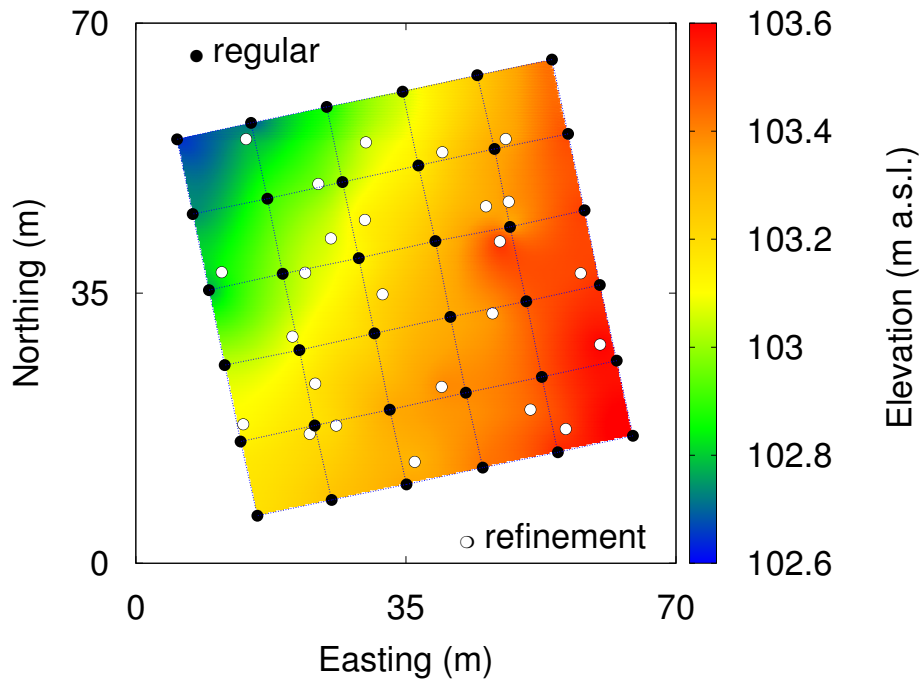


Fig. 1. Sampling grid at the 50×50m plot including sampling points on a regular grid with a mesh size of 10 m and randomly located sampling points for local refinement. Each sampling point represents a 50 cm and a 7 cm soil collar being closely located to each other.

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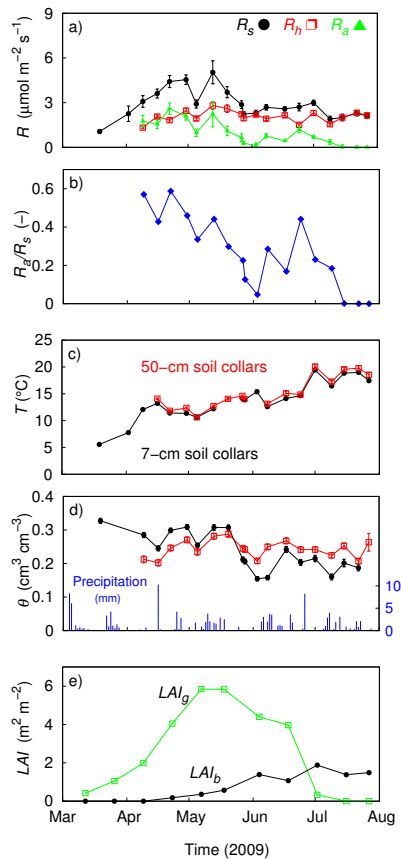


Fig. 2. Seasonal trend of **(a)** total (R_s), heterotrophic (R_h) and autotrophic respiration (R_a), **(b)** the contribution of R_a to R_s , **(c)** soil temperature (T) and **(d)** water content in 6 cm depth (θ) at locations of heterotrophic (red line) and total soil respiration (black line), and **(e)** green (LAI_g) and brown (LAI_b) leaf area index. Errorbars represent the 95% confidence interval.

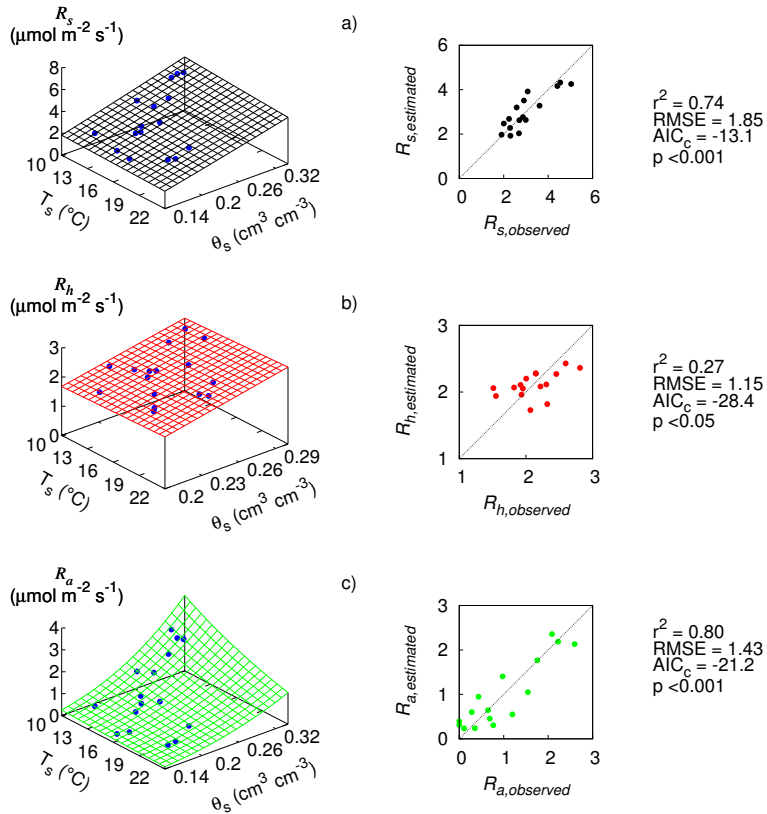


Fig. 3. Regression models of soil respiration related to soil temperature and water content. **(a)** Total soil respiration R_s related to soil temperature T_s and water content θ_s in 6 cm depth, **(b)** heterotrophic soil respiration (R_h) related to soil temperature T_h and water content θ_h in 6 cm depth, **(c)** autotrophic respiration R_a related to soil temperature T_s and water content θ_s in 6 cm depth. r^2 : coefficient of determination, RMSE: root mean square error, AIC_c : corrected Akaike Information Criterion, p : p-value.

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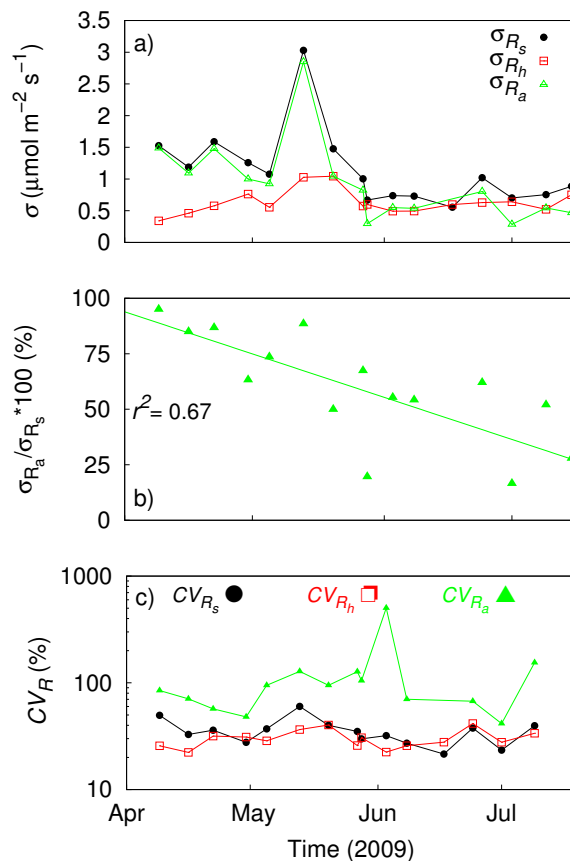


Fig. 4. Standard deviation of total (σ_{R_s}), heterotrophic (σ_{R_h}) and autotrophic respiration (σ_{R_a} , **(a)**), the autotrophic contribution to the spatial variations of total soil respiration **(b)** and **(c)** coefficient of variation (CV) of total (CV_{R_s}), heterotrophic (CV_{R_h}) and autotrophic soil respiration (CV_{R_a}); r^2 : coefficient of determination of linear regression in **(b)**.

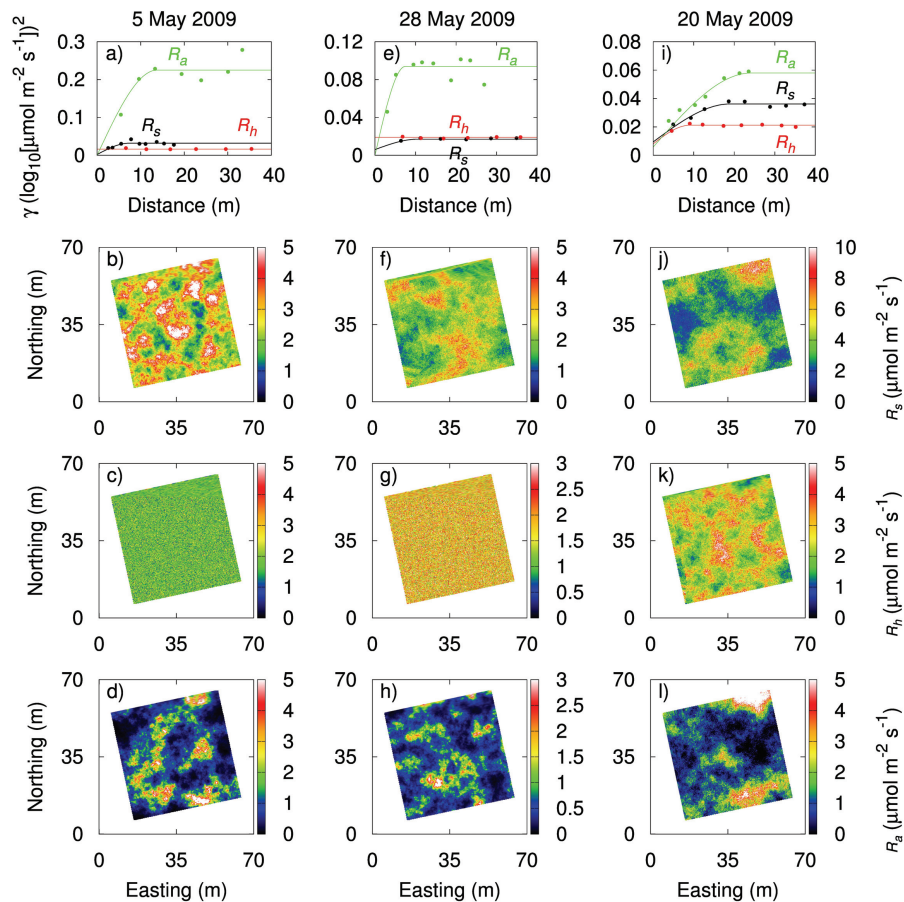


Fig. 5. Variograms and spatial patterns of total (R_s), heterotrophic (R_h) and autotrophic soil respiration (R_a) in winter wheat on 5 May 2009 (a–d), 28 May 2009 (e–h) and 20 May 2009 (i–l). Spatial patterns were calculated using conditional sequential Gaussian simulation.

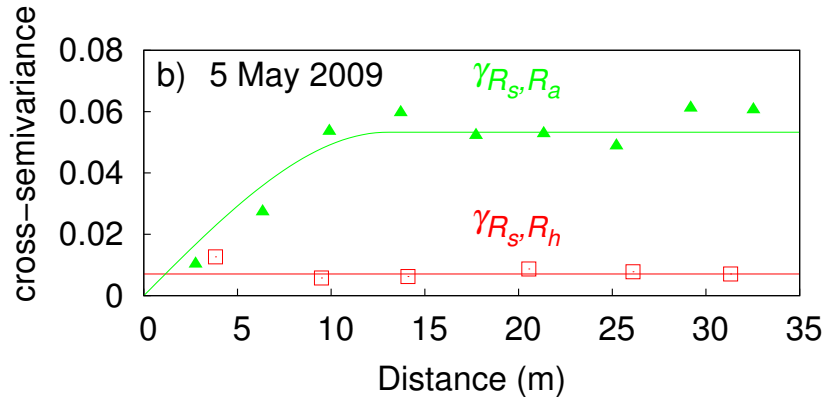
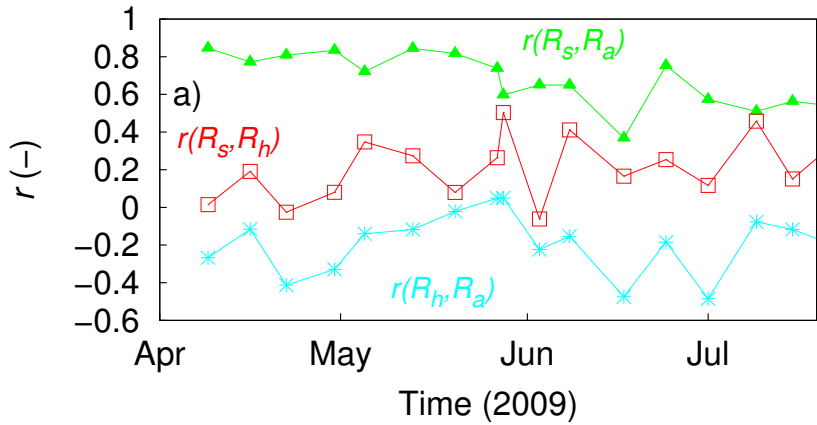


Fig. 6. Spatial correlation of total (R_s), heterotrophic (R_h) and autotrophic soil respiration (R_a) among each other. **(a)** Spatial correlation of R_s with R_h and R_a , respectively, and R_h with R_a during the season, **(b)** cross-semivariograms of R_s with R_h and R_a , respectively, on 5 May 2009.