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ORIGINAL PAPER

Leaf litter is an important mediator of soil respiration in an oak-dominated forest

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Abstract The contribution of the organic (O) horizon to total soil respiration is poorly understood even though it can represent a large source of uncertainty due to seasonal changes in microclimate and O horizon properties due to plant phenology. Our objectives were to partition the CO_2 effluxes of litter layer and mineral soil from total soil respiration (SR) and determine the relative importance of changing temperature and moisture mediating the fluxes. We measured respiration in an oak-dominated forest with or without the O horizon for 1 year within the Oak Openings Region of northwest Ohio. Mineral soil and O horizon respiration were subtracted from mineral soil respiration (MSR) to estimate litter respiration (LR). Measurements were grouped by oak phenology to correlate changes in plant activity with respiration. The presence of the O horizon represented a large source of seasonal variation in SR. The timing of oak phenology explained some of the large changes in both SR and LR, and their relationship with temperature and moisture. The contribution to SR of respiration from the mineral soil was greatest during pre-growth and pre-dormancy, as evident by the low LR:MSR ratios of 0.65±0.10 (mean ± SE) and 0.69±0.03, respectively, as compared to the other phenophases. Including moisture increased our ability to predict MSR and SR during the growth phenophase and LR for every phenophase. Temperature and moisture explained 85% of the variation in MSR, but only 60% of the variation in LR. The annual contribution of O horizon to SR was 48% and the ratio of litter to soil respiration was tightly coupled over a wide range of environmental conditions. Our results suggest the presence of the O horizon is a major mediator of SR.

Keywords Litter · Oak openings · Phenology · Soil respiration · Temporal variation

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Introduction

Respiration of terrestrial ecosystems makes an important contribution to the global carbon (C) cycle (Schimel 1995). Total belowground respiration from plant roots, mycorrhizas, and microbial decomposers can be used, in part, to estimate the potential of the ecosystem to store C in the soil. Efforts to estimate total soil respiration (SR) at larger spatial and temporal scales often rely on building empirical models based on in situ soil temperature and moisture (Lloyd and Taylor 1994; Davidson et al. 1998; Chen et al. 2004). However, a large source of uncertainty remains in accurately estimating SR because the underlying mechanisms by which plant phenology, temperature and other environmental factors mediate SR are unclear.

Within a terrestrial ecosystem, the primary uncertainty in estimating SR is the complex influence and interaction of autotrophic (Ra) and heterotrophic (Rh) respiration. Partitioning the contribution of each of these factors to SR

remains difficult because environmental factors vary greatly at different temporal and spatial scales (Hanson et al. 2000). For example, the apparent sensitivity (i.e., Q_{10}) of root respiration to soil temperature is almost twice as large as in root-free soil (Boone et al. 1998). Furthermore, the sensitivity of SR to environmental factors changes seasonally as the amount and availability of C input change (Davidson et al. 1998; Janssens and Pilegaard 2003; DeForest et al. 2006); these environmental factors can be recognized in predictive models when certain thresholds are reached (Ma et al. 2005). Respiration rates from the mineral soil and the organic (O) horizon are uncertain due to varying differences in substrate availability (Boone et al. 1998; Chen et al. 1999). Furthermore, the O horizon can physically buffer the mineral soil from changes in temperature and moisture (Chen et al. 1999). However, we understand only poorly how changes in plant phenology, and thus the flow of substrate belowground, will influence the relationship between O horizon respiration (i.e., litter respiration; LR) and biophysical controls. The confounding mixture of different substrates, trophic organisms, seasonal changes in microclimate, and activity makes it difficult to predict SR using empirical models of mechanistic controls.

Annual SR efflux accounts for around two-thirds of ecosystem respiration in forests, and is equally split between Ra and Rh (Hanson et al. 2000; Sanderman et al. 2003). However, we have relatively little in situ data on contribution dynamics of these two trophic groups at different temporal scales—seasonally and annually (Tang et al. 2005)—especially when plants are dormant. Respiration from litter has a greater dependency on moisture than temperature, but LR contribution to SR depended on the frequency and amount of precipitation (Hanson et al. 2003). For example, Borken et al. (2003) reported that LR was a minor component of respiration, but after precipitation it can dominate SR for several days until the O horizon dries. Therefore, LR may be a large source of uncertainty when estimating SR because of the highly ephemeral nature of LR. For this reason, soil temperature and moisture may be poor metrics for predicting LR.

To understand how LR and SR respond independently to environmental conditions, we measured seasonal respiration with and without the O horizon in an oak-dominated forest in northwest Ohio in the United States. Partitioning SR into a mineral soil and O horizon components on a seasonal time scale can significantly enhance our capability of predicting the magnitudes and variation in SR. We hypothesized that autotrophic activity would have the greatest influence, as compared to heterotrophic respiration, on mineral soil respiration (MSR) directly from either roots, mycorrhizas, or metabolized exudation. Furthermore, heterotrophic respiration, when compared to autotrophic respiration, has the greatest influence on O horizon respiration. Therefore, we expect the ratio of O horizon respiration (i.e., LR) to autotrophic respiration (i.e., MSR) to be lowest in summer, and greatest in winter. Our study objectives were to determine: (1) the magnitudes and dynamics of LR, MSR, and SR through manipulations of litter horizon in an oak-dominated forest, (2) the relative importance of temperature and moisture mediating MSR and LR, and (3) how this mediation changes seasonally as determined by plant phenophases.

Materials and methods

Study site

Our study site was located in an oak-dominated forest within the Oak Openings Region of northwest Ohio (N41° 33′47″ by W83°50′58″). This ecosystem is a mosaic of oak savanna, barrens, and wet prairie that developed on a series of sandy glacial beach ridges and swales over fine texture till (Moseley 1928; Brewer and Vankat 2004). Our study area is within the 1,500 ha Metroparks of Toledo Area Oak Openings Preserve. The mean annual temperature is 9.2°C and annual precipitation is 840 mm. The soils are sandy mixed, mesic, Spodic Udipsamments. The bulk density is approximately 1.24 g cm^{-3} and soil texture is sand. Soil C and N content in the top 20 cm are 28.1 g C kg^{-1} and 1.6 g N kg^{-1}. The O horizon biomass ranged from 850 g m^{-2} during the summer to 1,300 g m^{-2} shortly after leaf fall. The tree species composition by biomass included *Quercus* spp. (80%), *Acer rubra* (13%), and *Prunus serotina* (7%). The woody groundcover is primarily *Vaccinium* spp., with very few tree seedlings. Within the study area, we continually measured 30-min mean air temperature (T_a; °C), soil temperature at 5 cm depth (T_s; °C), O horizon temperature (T_O; °C), and soil water potential (SWP; MPa). Precipitation was recorded using a TE525 tipping bucket rain gauge (Texas Electronics, Dallas, TX) installed on an eddy-covariance flux tower located within the study site (DeForest et al. 2006; Noormets et al. 2008)

Phenology

Tree phenology was recorded on four major phases (i.e., pre-growth, growth, pre-dormancy, and dormancy) of *Quercus* spp. following DeForest et al. (2006). Briefly, pre-growth phase was defined by *Quercus* spp. flowering and bud break, and was considered a period of high root production and the start of acorn production. The start of the growth phase was defined by 95% leaf flush for *Quercus*. The start of the pre-dormancy phase was visually determined by the start of leaf discoloration of the *Quercus* spp., but leaves were still on the branches. The start of

dormancy phenophase was defined by a 95% loss of foliage from the *Quercus* spp. Phenology was used to delineate the year into periods that casually represent differences in the quality and amount of substrate entering the O horizon or mineral soil.

Litter exclusion

To determine the contribution of LR to SR, we removed the Oi and Oe horizons by hand on 1 July 2005. SR was measured in this exact area prior to litter removal, with rates similar to those from other plots (DeForest et al. 2006). Litter was removed from a 4 m^2 area and the fine litter fraction was allowed to dry over several days; the remaining litter was removed with a power shop vacuum. This method caused no noticeable physical disturbance to the mineral soil. Remaining fine roots from the O horizon were also carefully removed. Six plastic collars with a diameter of 10 cm were placed into the soil 2 cm deep at least 30 cm apart and the entire area was covered with ~3 cm brown rubber mulch that was similar to the size and shape of wood mulch. The rubber mulch was washed several times with water to remove any potential contaminants. Rubber mulch was used to simulate the buffering properties of the O horizon on soil temperature and moisture without providing substrate for microbial metabolism. However, the rubber mulch did not simulate the high water holding capacity of litter, so it is likely more precipitation water entered the soil with the rubber mulch treatment. Throughout the experiment, aboveground litter was removed if it fell into or outside the collars. During leaf fall, a tent made from shade cloth was established to allow precipitation to pass through, but prevented litter from falling or leaching on to the rubber mulch treatment plots. Six SR collars were established, with an intact O horizon, 4 m from the litter exclusion collars. While the control plots were measured for SR, the litter-excluded plots measured MSR. The difference between the two is considered as the respiration from the litter layer (i.e., LR).

CO_2 efflux

Respiration was measured a total of 69 times at all 12 collars over the course of a year starting on 29 July 2005 using a portable infrared gas analyzer (LI-6400, Licor, Lincoln, NE). Measurements were made at least weekly starting from the growth, pre-dormancy, and dormancy phenophase. During the pre-growth phenophase, measurements were typically made bi-weekly. Before each sampling session, we zeroed the LI-6400, if necessary, and desiccant and soda lime were checked frequently. Respiration was measured in early afternoon during most weather conditions, except during heavy rain. Throughout the winter, the LI-6400 and chamber were encased in aluminum bubble wrap insulation to protect it from freezing. Snow over 1 cm deep was removed from the collar and allowed to vent for a few minutes prior to measurement. The snow was placed back immediately after each measurement. During measurements, soil temperature (T_s) was recorded at 5 cm in the soil within 10 cm of the collar, and soil moisture was measured once for each of the treatments. The temperature of the O horizon (T_O) was measured in between the Oi and Oe horizons near each of the soil collars. We sampled the Oi and Oe horizon three times from a 625 cm^2 sampling frame for each respiration measurement to estimate litter water content (LWC; g H_2O g $litter^{-1}$). We determined litter water potential (LWP; MPa) using LWC and the model developed by Hanson et al. (2003) for oak litter:

$$LWP = -1 \cdot \left[5.53 \cdot 10^8 \cdot 504.85^{\left(-3.22 \cdot LWC^{0.0528}\right)}\right] \quad (1)$$

Data analysis

The selection of these equations for a specific phenophase was determined by comparing the residuals with spot measurements by linear regression analyses. Selection criteria were deduced from model results that produced minimal spread of residuals over measurements with minimal bias. The temperature-dependence of respiration was expressed using a non-linear least squares regression (PROC NLIN, SAS; http://www.sas.com/) as a function of temperature (Lloyd and Taylor 1994; Law et al. 2002):

$$SR = R_{10} \cdot e^{\frac{Ea}{R}\left(\frac{1}{T_{ref}} - \frac{1}{T}\right)} \quad (2)$$

where SR is soil or MSR (μmol CO_2 m^{-2} s^{-1}), E_a is activation energy (kJ mol^{-1} K^{-1}), R is a universal gas constant (8.3134 J mol^{-1} K^{-1}), and R_{10} is the reference respiration, normalized to a common temperature (T_{ref}= 283.15 K, i.e., 10°C) whereas T is soil temperature in °C. Equation 2 was used for modeling SR and MSR in non-growth phenophases. Because SWP significantly ($P<0.01$) influenced MSR during the growth phenophase, and to improve the model fit, we modified Eq. 2 to incorporate SWP into a new non-linear model:

$$MSR = R_{10} \cdot e^{\frac{Ea}{R}\left(\frac{1}{T_{ref}} - \frac{1}{T}\right)} \cdot \left(sa \cdot sb^{SWP}\right) \quad (3)$$

where sa is a constant and SWP is soil water potential (MPa). The following model, which was developed by Hanson et al. (2003), was used to estimate LR within LWP:

$$LR = \left(la \cdot lb^{LWP}\right) \cdot e^{\frac{Ea}{R}\left(\frac{1}{T_{ref}} - \frac{1}{T}\right)} \quad (4)$$

where LR is litter respiration (μmol CO_2 m^{-2} s^{-1}), la and lb are constants within a phenophase, and LMP is litter matric

potential (MPa) calculated from LWC and LWP on *Quercus* leaves (Hanson et al. 2003). LR was calculated from the difference between SR and MSR. Therefore, LR is more of a metric of the presences of the O horizon influencing SR rather than actual respiration from the O horizon because we did not account for the potential synergic effect between soil and the O horizon. We applied the following equation (Eq. 5) for SR during the growth phenophase because SWP and LWP exerted a strong influence on respiration and this improved the model fit:

$$SR = \left(la \cdot lb^{LWP}\right) \cdot e^{\frac{Ea}{R}\left(\frac{1}{T_{ref}}-\frac{1}{T}\right)} + \left(sa \cdot sb^{SWP}\right) \quad (5)$$

where SR is total soil respiration (μmol CO_2 m^{-2} s^{-1}) during the growth phenophase and the parameters are the same as described in the above equations. In order to test the model, we randomly selected half the data from each of the phenophases and used 35 sampling dates for model development and the remainder for testing. We were unable to test the model for pre-dormancy because its total sample size was four. A simple linear regression was using to compare predicted respiration with measured respiration.

Results

Soil respiration rates were highest and most variable during the growth phenophase compared to the other phenophases (Fig. 1). SR declined steadily for 5 months from the start of the pre-dormancy phenophase independent of soil temperature. After 5 months, an unseasonably warm period (i.e., + 5°C for 3 days) in mid-March disrupted the pattern. The seasonal pattern of SR was similar to MSR; however, early in the dormancy phase, SR was near 3 μmol CO_2 m^{-2} s^{-1}, which was similar to the mean rates of pre-dormancy and pre-growth phenophases. This increase in SR was attributed to LR because MSR varied little throughout dormancy. SR was similar to MSR only when the O horizon was below −1°C (Fig. 1). LR increased despite declining temperatures around 30 days after leaf fall (Fig. 1).

The contribution to SR of respiration from the mineral soil was greatest during pre-growth and pre-dormancy, as evident by the low LR:MSR ratios of 0.65±0.10 (mean ± SE) and 0.69±0.03, respectively, as compared to the other phenophases. While the LR:MSR ration in growth phenophases varied little at 0.91±0.06, the ratio was significantly ($P<0.01$) greater during the dormancy phenophase, at 1.47± 0.18. Overall, MSR accounted for the largest portion of SR during all but the dormancy phenophase. Within a phenophase, the relationship between LR and MSR was tightly coupled over a wide range of O horizon temperatures and moisture conditions. The LR:MSR decoupled (i.e., 0.5<LR:SR>1.5) when the O horizon was frozen or when O horizon moisture was less than 50% during the growth phase.

The importance of litter moisture as a factor controlling SR was highest during the dormancy phenophase as evident by the greater coefficients associated with moisture in Eq. 4 (Table 1). The pre-dormancy phenophase had the lowest coefficients whereas the growth and pre-growth coefficients were similar to each other. The temperature sensitivity (i.e., E_a) was similar for most phenophases, except pre-dormancy, which had the highest value (Table 1). The R_{10} of MSR was highest and most varied during the pre-dormancy

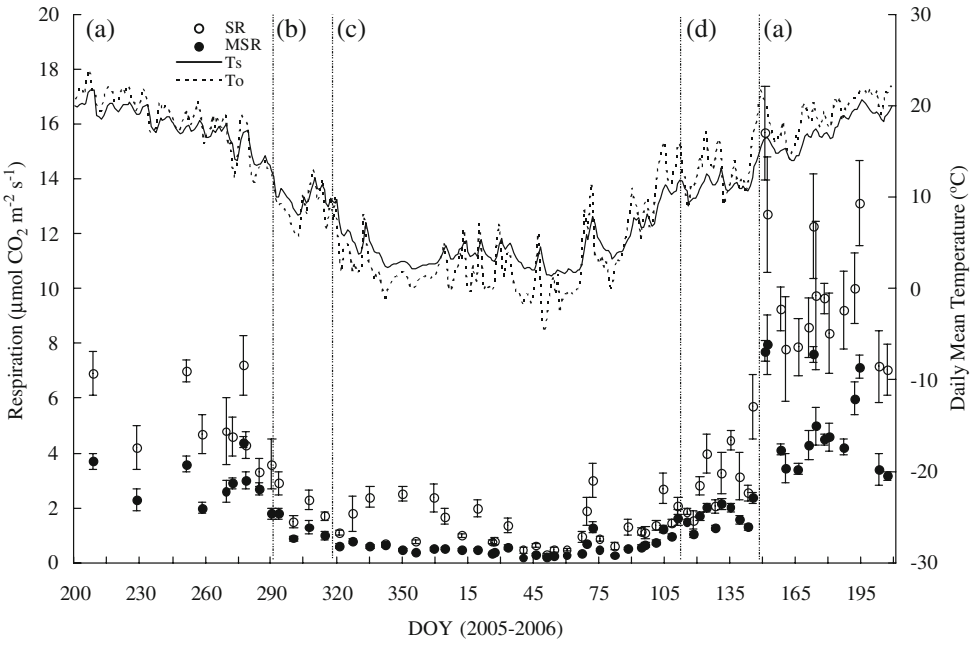

Fig. 1 Seasonal variation in total soil respiration (SR; *open circles*) and mineral soil respiration (MSR; *closed circles*) (μmol CO_2 m^{-2} s^{-1}) based on 69 spot measurements between 2004 and 2005. *Error bars* 1 standard error of the mean (n=6); *solid line* daily mean soil temperature (T_s; °C); *dashed line* oxygen (O) horizon temperature (T_o; °C); *vertical dotted lines* phenophase transitions: *a* growth phenophase, *b* pre-dormancy, *c* dormancy, *d* pre-growth

Table 1 Model parameters of litter, soil, and mineral soil respiration calculated for the four phenophases. R_{10} Respiration (μmol CO_2 m^{-2} s^{-1}) at 10°C; *la*, *lb* parameters from litter water potential (MPa); *sa* parameters from soil water potential (MPa); E_a activation energy (= apparent temperature sensitivity of respiration); *P-values* significance of model (values in parenthesis indicate 1 SE of the mean)

	R_{10}	la	lb	sa	E_a	*P*-value
Litter respiration						
Phenophase						
Growth		2.37 (0.72)	1.08 (0.08)		43,791 (23,791)	<0.01
Pre-dormancy		0.46 (0.03)	0.36 (0.03)		89,139 (8,156)	0.02
Dormancy		5.17 (2.97)	7.41 (5.67)		45,600 (16,405)	<0.01
Pre-growth		2.21 (0.55)	1.80 (0.34)		40,328 (32,598)	<0.01
Mineral soil respiration						
Phenophase						
Growth	2.32 (0.55)			1.05 (0.02)	70,299 (19,987)	<0.01
Pre-dormancy	1.36 (0.23)				102,265 (115,098)	0.05
Dormancy	1.00 (0.05)				76,384 (7,154)	<0.01
Pre-growth	1.28 (0.09)				85,439 (18,424)	<0.01
Soil respiration						
Phenophase						
Growth		4.69 (1.12)	1.07 (0.05)	1.03 (0.01)	69,997 (20,380)	<0.01
Pre-dormancy	2.29 (0.34)				102,243 (102,620)	0.04
Dormancy	2.24 (0.26)				63,574 (14,385)	<0.01
Pre-growth	2.14 (0.37)				88,509 (43,645)	<0.01

phenophase, followed by pre-growth, dormancy, and growth (Table 1). The growth phenophase R_{10} was lowest as SMP was accounted for in Eq. 3. The E_a was highest during the growth and pre-dormancy phenophases, followed by the pre-growth and dormancy phenophase (Table 1). Soil respiration R_{10} was similar among the previously mentioned phenophases. E_a was not significantly different ($P<0.05$) among the phenophases. When comparing respiration from the difference sources (i.e., SR, MSR), E_a was generally lower for LR that for SR and MSR.

Temperature changes in the litter and soil explained most of the variation between 50 and 80% in SR, MSR, and LR. Temperature was highly correlated with variation in MSR below 10°C as evident by small residuals (Fig. 2). T_O explained LR below 10°C, but residuals varied more than for MSR (Fig. 2). While SWP explained MSR well (i.e., low residuals) over a wide range of values, LWP explained variation in LR best below −0.75 MPa (Fig. 2). Above −0.75 MPa, the spread of residuals increased, but stayed within 1.0 μmol CO_2 m^{-2} s^{-1}. The correlation for temperature to explain the variation in respiration was weakest during the growth phenophase, when the amount of soil moisture became more important to SR. Incorporating SWP into the model improved our ability to explain variation in MSR as evident by an increased r^2 (from 0.25 to 0.71). Likewise, incorporating SWP and LWP into the model significantly improved our ability to explain SR during the growth phenophase (i.e., r^2 increased from 0.23 to 0.58) or annually (i.e., r^2 increased from 0.75 to 0.84). For all phenophases, LWP was always a significant ($P<0.01$) factor influencing LR. However, this influence was most pronounced when litter was dry rather than wet. For example, when litter was at field capacity, LWP explained less of the variation in LR than when LWP was less than half field capacity (Fig. 2).

Accounting for phenophases, the models based on temperature and water potential predicted measured respiration very well (Fig. 3). When comparing measured respiration with predicted respiration, r^2 was 0.60, 0.85, and 0.84 for LR, MSR, and SR, respectively. The slope was 0.52, 0.60 and 0.61 for LR, MSR and SR, respectively. The intercept, a measure of potential bias, for LR, MSR and SR was 0.78, 0.56, and 1.02, respectively. Most of the deviation from MSR and SR modeled respiration was during the first three sampling times of growth phenophase in 2006 when soil temperature increased dramatically from the weeks before (e.g., 11°C to 18°C) and respiration rates were within the top 5% highest respiration rates of the study (Figs. 1, 3).

Discussion

Annual SR is typically represented by a general bell-shaped curve centered around the growth phenophase (Davidson et al. 1998; Janssens and Pilegaard 2003; Lee et al. 2003; Hanson et al. 2004; Yuste et al. 2004). Despite declining temperatures, we observed an increase in SR for 2 months following full leaf senesce that corresponded with an input of fresh litter decay (Fig. 1). We are unaware of many studies that reported increased SR following full leaf

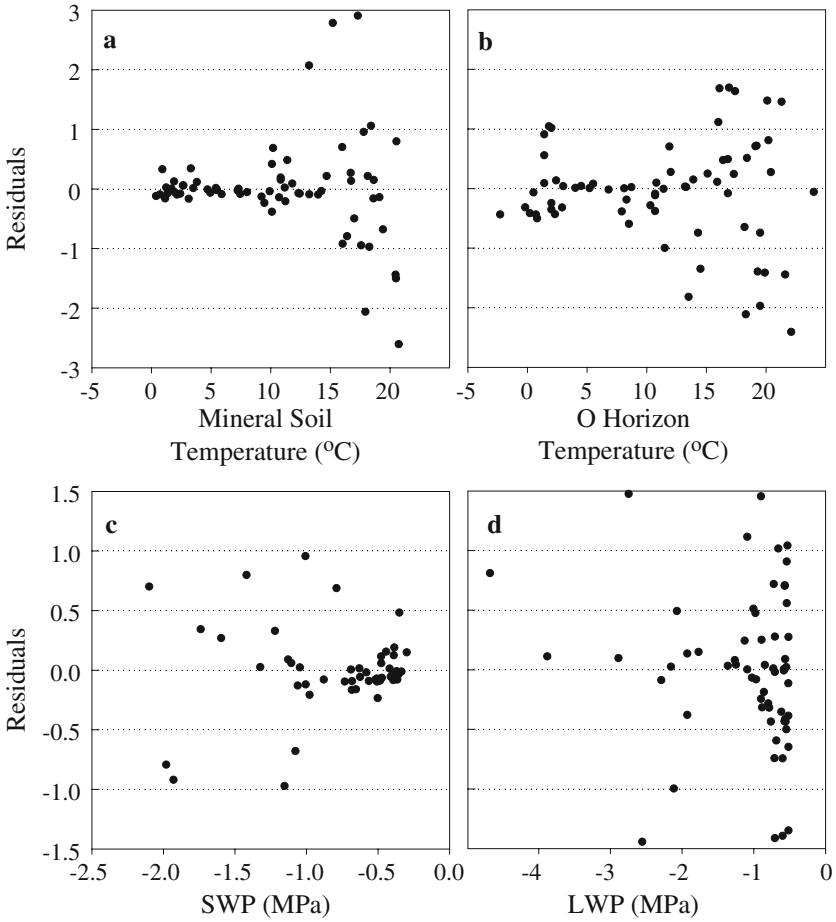

Fig. 2 Changes in residuals of the Arrhenius model (Eqs. 3, 4) with **a** mineral soil temperature, **b** T_o, **c** soil water potential (SWP; MPa), and **d** litter water potential (LWP; MPa)

senesce reported elsewhere because it is rare to measure SR frequently in situ in winter (Granier et al. 2000). Nevertheless, we reason that this pulse in respiration is common, but the timing of the pulse may be variable and depend on seasonal changes in local microclimates. DeForest et al. (2006) measured SR the previous winter near this study site but did not observe this pattern, although the pattern was observed in this winter in a continuation of the experiment as described in DeForest et al. (2006). The discrepancy between increased SR and leaf senesce may be because the dormancy phase during this experiment was 2–5°C warmer than the previous dormancy phase. It is possible that the warm environment in the fall of 2005 allowed for increased LR in the early dormancy phase when litter is typically frozen, whereas in a normal (i.e., cooler) year LR is highest during the spring thaw. Regardless of low temperatures, litter decomposition and microbial activity have been observed under snow cover (Brooks et al. 2005; Uchida et al. 2005). Therefore, local environmental conditions (e.g., soil microclimate) can play an important factor in the timing of fresh litter respiration. In the context of warming soils, the observed shift in this respiratory pulse could have implications on the cycling of nutrients released from decomposition.

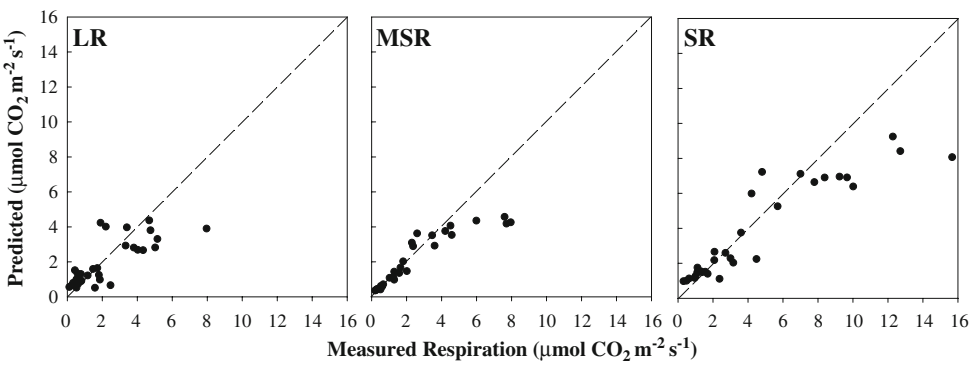

Fig. 3 Comparison of measured and modeled litter respiration (LR), MSR, and SR based on temperature and soil and litter moisture (when appropriate). The measured respiration data is independent of the data used for model development. *Dashed line* 1:1 ratio

Although different trophic groups and exposures to changing temperature and moisture dominate the O horizon and mineral soil, the relationship between LR and MSR were tightly coupled over a wide range of microclimatic conditions and phenophases. Overall, the mean respiration from the presences from the O horizon was 48% (± 12%) of SR when below freezing observations were excluded. Moreover, the LR:MSR ratios between pre-dormancy, pre-growth, and growth phenophase were similar ($P>0.05$) even though soil temperature differed by 10°C and the O horizon was frequently dry during the growth phenophase (Fig. 1). The results suggest that an interaction exists between the mineral and organic horizons that is influenced by the same microclimatic conditions. Potentially, fine roots or mycorrhizas from the soil in the O horizon could influence the close connection as they colonize the rubber mulch. Likewise, the methods used to estimate LR might be a better metric of the presence of the O horizon on SR than the actual respiration from the O horizon. For example, leachate from the O horizon can supply labile material that will stimulate MSR (Borken et al. 2003; Sulzman et al. 2005). We observed greater measured than modeled estimates (~8 vs ~4 μmol CO_2 m^{-2} s^{-1}) of MSR after heavy rains (i.e., >15 mm day^{-1}) in early June, which would support the hypothesis of O horizon leachate of labile C increasing SR. Nevertheless, even following a heavy rain, the LR:MSR ratio was similar to the annual mean, suggesting that LR and MSR respond to heavy rain in a similar manner. While the apparent sensitivity of LR to temperature (i.e., E_a) was lower, the sensitivity to water potential was higher. However, these differences did not translate into large differences in respiration responses to environmental conditions. The only phase where we observed a decoupling of LR and MSR was shortly after full leaf senesce, when LR increased due to the decomposition of fresh litter even as MSR steadily declined, or when LR was minimal when O horizon temperature fell below −1°C (Fig. 2).

Phenophase altered the importance of temperature and moisture mediating MSR and LR. These results are consistent with those of previous studies (Davidson et al. 1998; Janssens and Pilegaard 2003; Yuste et al. 2004; DeForest et al. 2006). During the growth phenophase, the influence of temperature mediating MSR and SR declined, as moisture became more significant (Table 1). Likewise, during the 2 months after full leaf senesce, SR was at a similar level to observed rates at temperatures 5–10°C higher due to the addition of fresh litter (Fig. 1). During this time period, estimated LR was poorly correlated with measured values, suggesting the large influence of substrate quality on LR could not be explained by temperature or moisture (Brooks et al. 2005; Sulzman et al. 2005; Uchida et al. 2005). Soil moisture is frequently used to explain the variation in SR and ecosystem respiration (Hanson et al. 1993; Noormets et al. 2008). However, litter moisture has rarely been used to help explain the variation in soil respiration (Borken et al. 2003; Hanson et al. 2003). We propose that, during the growing season, models used to estimate SR should incorporate parameters that also account for factors that influence LR in order to increase the model prediction as found here or in Hanson et al. (2003). Generally, the O horizon represents nearly 50% of the variation in SR even though our O horizon C pool is 16-fold smaller than that found in the mineral soil. Our dynamic modeling approach adjusts parameters and models in accordance with phenophase and substrate and was effective in estimating respiration, especially when SR was below 8 μmol CO_2 m^{-2} s^{-1}, or when temperature was below 15°C (Fig. 3).

Conclusions

The presences of the O horizon represent a large source of respiration and seasonally variation in SR. We found that the timing of oak phenology was critical in predicting all respiration terms and could explain some of the large changes in both SR and LR, and also explain their relationship with temperature and moisture. The observed increase in SR from the O horizon shortly after the start of dormancy phenophase suggests that active decomposition is occurring in the O horizon even in cold environments. While the LR and SR ratio decoupled during the dormancy phenophase where LR:MSR was highest, LR and MSR appeared tightly coupled for most of the year and varied little.

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